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Late Wisconsinan and Holocene Fauna from Smith Creek Canyon, Snake Range, Nevada

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Abstract. During the late Pleistocene, montane glaciers in the Snake Range, eastern Nevada reached an elevation as low as 2900 m and pluvial Lake Bonneville rose to approximately 1580 m, only 130 m below the entrance of the east-facing Smith Creek Canyon. It is not known whether the two events coincided. Packrat midden macrofossils indicate that bristlecone pine (*Pinus longaeva*), limber pine (*P. flexilis*), and other subalpine taxa dominated the plant communities in Smith Creek Canyon through the late Wisconsinan. We report here 2 fish, 4 anurans, 9 lizards, 8 snakes, and 15 small mammals recovered from 15 packrat middens and a pollen profile from cave fill. This assemblage adds 15 amphibians and reptiles and 7 mammals to the approximately 46 terrestrial animals previously known from the late Pleistocene and early Holocene of the canyon. Dung pellets of the locally extirpated pika (*Ochotona* cf. *princeps*) were found in five packrat middens. A single tooth of the heather vole (*Phenacomys* cf. *intermedius*) from Smith Creek Cave is the first late Pleistocene record for this genus in the Great Basin. We review and update the late Pleistocene and Holocene fauna from 4 caves and 2 shelters in Smith Creek Canyon.

Introduction

The Snake Range of White Pine County, eastern Nevada, is a north–south trending mountain 80 km long. Smith Creek Canyon, a deep canyon on the eastern face of this Great Basin range, opens onto the Lake Bonneville playa in the Snake Valley of Utah. During the late Pleistocene, montane glaciers reached elevations as low as 2900 m in the Snake Range (Drewes 1958), and pluvial Lake Bonneville rose to a level of approximately 1580 m, only 130 m below the entrance of Smith Creek Canyon. If the late Wisconsinan glacial maximum coincided with the high stand of Lake Bonneville, biotic communities in this canyon would have been restricted to an elevational range of less than 1310 m (Fig. 1).

Fossil localities.—Late Pleistocene vertebrate fossils from Smith Creek Canyon, specifically Smith Creek Cave, were reported by M. Harrington (1934) from the Southwest Museum and by others since. In 1955, T. E. Downs and associates from the Natural History Museum of Los Angeles County (LACM), California, screened some of the cave sediments. Field notes of the LACM indicate that the cave contained little or no stratification (Brattstrom 1976). Howard (1935, 1952) described a new species of extinct eagle (*Spizaetus willetti*) and a teratorn (*Teratornis incredibilis*) and listed the Smith Creek Cave avifauna, unfortunately giving the stratigraphic associations only as from the older deposits of the lower levels. Stock (1936) described a new species of extinct mountain goat (*Oreamnos harringtoni*), but again did not discuss placement within the stratigraphic sequence. Brattstrom (1958, 1976) reported amphibians and reptiles from the cave sediments and Goodrich (1965) updated the list of the entire fauna (amphibians, reptiles, birds, and mammals); again the stratigraphy and temporal associations were only scantily discussed.

Bryan (1979*a*) made further excavations in the cave in search of evidence for Early Man and for the first time described the stratigraphy within a portion of the cave.

FIGURE 1. Map of Nevada and bordering states showing Smith Creek Canyon (1) and Gatecliff Shelter (2) along with Great Salt Lake (black) and Lake Bonneville (stippled) at the 1580 m elevation.

Miller (1979) identified the mammalian fauna recovered during Bryan's excavations, providing another updated listing of the fauna; some stratigraphic associations were given. Both Bryan (1979*a*) and Miller (1979) emphasized the deposits and fauna associated with Man, those units dating less than 11 500 B.P. Thus no comprehensive stratigraphic analysis of the fauna has been published.

In 1977 and 1978 we visited Smith Creek Canyon to study fossil packrat (*Neotoma*) middens and to collect a pollen profile from the Smith Creek Cave sediments. Plant remains from some of these middens are discussed in a previous report (Thompson 1979), and other assemblages are still being analyzed (RST). The packrat midden fossils document that bristlecone pine (*Pinus longaeva*), limber pine (*P. flexilis*), and other subalpine taxa dominated the plant communities in Smith Creek Canyon throughout the late Wisconsinan. The Smith Creek Cave pollen profile provided little paleoenvironmental information and could not be dated directly. In this report we describe the fish, amphibians, reptiles, and mammals recovered from 15 packrat middens from Smith Creek Canyon and in association with the pollen profile, and the herpetofauna recovered by Bryan (1979*a*, Miller 1979) in his excavation in Smith Creek Cave. We also review the entire local fauna recovered from all archaeological and paleontological

investigations in Smith Creek Canyon and attempt to place these records in the correct paleoenvironmental and chronological context.

Local setting.—The lower concourse of Smith Creek Canyon is a steep-walled east–west trending canyon incised into Paleozoic limestone. In this part of the canyon there are numerous caves, including those described below in which we have found our fossil materials. The upper reaches of Smith Creek Canyon are lined with other Paleozoic sedimentary rocks and Mesozoic intrusives. We have not located any caves or fossil packrat middens in this area. The intermittent waters of Smith Creek are primarily derived from the elevated plateau surrounding Mount Moriah (3673 m).

Although the vegetation in Smith Creek Canyon is broadly divided into elevational zones, the major slope and aspect contrasts between the north and south facing slopes create numerous microenvironments for plants of higher and lower elevations. At the canyon entrance the plant community is dominated by shadscale (*Atriplex confertifolia*) and other xerophytes, including spiny hopsage (*Grayia spinosa*), greasewood (*Sarcobatus vermiculatus*), rabbitbush (*Chrysothamnus nauseosus*), Mormon tea (*Ephedra nevadensis*), horsebrush (*Tetradymia axillaris*), Harriman yucca (*Yucca harrimaniae*), and bud-sage (*Artemisia spinescens*). These same taxa are dominant in the Snake Valley to the east and also are common on xeric slopes throughout Smith Creek Canyon.

Sagebrush (*Artemisia tridentata, A. nova*) occurs both in nearly pure stands in the canyon bottom and as a common understory element in the pinyon-juniper woodlands and forested communities. Utah juniper (*Juniperus osteosperma*) and single needle pinyon (*Pinus monophylla*) occur throughout the limestone walled part of the canyon and form denser stands on the north facing slopes and on alluvium. Little leaf mountain mahogany (*Cercocarpus intricatus*), greasebush (*Forsellesia nevadensis*), skunkbush (*Rhus trilobata*), and joint-fir (*Ephedra viridis*) are common in the pinyon-juniper woodland and are often dominant on xeric slopes and on limestone substrates.

Montane and subalpine conifers, including white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), ponderosa pine (*Pinus ponderosa*), limber pine, and bristlecone pine, are present at relatively low elevations in mesic niches on the north facing slope and along the upper concourse of Smith Creek. Other common riparian plants include narrowleaf cottonwood (*Populus angustifolia*), willows (*Salix* spp.), water birch (*Betula occidentalis*), chokecherry (*Prunus virginiana*), Rocky Mountain maple (*Acer glabrum*), Rocky Mountain juniper (*Juniperus scopulorum*), and wild rose (*Rosa woodsii*). The higher elevations of the northern Snake Range support groves of quaking aspen (*Populus tremuloides*) and stands of bristlecone pine and limber pine on rocky outcrops.

Although the fossil localities we investigated occur in a narrow elevational range (1860 m to 2060 m), the variations in slope and aspect at these sites place them in different environmental settings (Table 1). Smith Creek Cave (1950 m elev.) and Ladder Cave (2060 m elev.) are on a steep south facing slope at the entrance to the canyon and are surrounded by a xeric pinyon-juniper woodland with an abundance of xerophytic plants (*see* Thompson 1979). Streamview Shelter is on a protected north facing slope near the canyon bottom (1860 m elev.), and Council Hall Cave is higher (2040 m elev.) on the same slope. These two sites are in a relatively dense pinyon-juniper woodland, with fewer xerophytes than on the opposing slope. Montane and subalpine conifers occur in protected niches near both Council Hall Cave and Streamview Shelter. Amy's Shelter and the Kachina Cave are in the bottom of the canyon by the creek. These two sites probably were buried by alluvium during the last full-glacial, only to be exposed during the latest phases of the late glacial or early Holocene.

Methods

The Smith Creek Canyon localities included within this report are Smith Creek, Ladder, Council Hall, and Kachina caves, Amy's Shelter and the packrat midden rockshelter we named Streamview.

TABLE 1. Paleontological and archaeological sites in Smith Creek Canyon, Snake Range, and the adjacent Snake Valley, Nevada, that are discussed in text.

Locality	Slope	Elevation	Type of deposit	Age range (yr B.P.)	Present status
Smith Creek Cave	South-facing	1950 m	Archaeological and non-archaeological cave sediments; 4 packrat middens	≥12 500 to 1000	Relatively xeric site, sparse pinyon-juniper woodland, active talus formation, high above canyon bottom
Ladder Cave	South-facing	2060 m	6 packrat middens	27 000 to 11 000	Relatively xeric site, sparse pinyon-juniper woodland, active talus formation, high above canyon bottom
Amy's Rockshelter	North-facing	1740 m	Archaeological cave sediments	5000 to 1500	In canyon bottom near entrance, relatively arid, scattered juniper with sagebrush-shadscale shrub
Streamview Rockshelter	North-facing	1860 m	3 packrat middens	17 000 to 6500	Ca. 15 m above canyon bottom, pinyon-juniper
Kachina Cave	North-facing	1770 m	Archaeological cave sediments	ca. 4500 to present	Along streamside of intermittent Smith Creek, pinyon-juniper and riparian vegetation
Council Hall Cave	North-facing	2040 m	Cave sediments; 2 packrat middens	24 000 to 4000	High above cayon bottom, relatively mesic site, pinyon-juniper with scattered subalpine conifers, little active talus formation
Garrison	North-facing	1640 m	Small overhang; 2 packrat middens	13 500 to 12 000	Small rock outcrop in the middle of Snake Valley, desertscrub, little active talus

Packrat middens.—All fossil packrat middens in this report were well-indurated with urine. To insure that stratigraphic units of different ages were not mixed during sampling, each midden was examined carefully prior to collection. Approximately two kilograms were removed from each stratigraphic unit and packaged in the field. In the laboratory approximately one kilogram of each unit was soaked in water until the cementing urine dissolved. The disaggregated samples were then washed through 20-mesh screens and oven dried. The fossils were hand-sorted, and after identification, plant remains were selected for radiocarbon dating and pretreated with 10% HCl in an ultrasonic cleaner. Radiocarbon dates from the packrat middens and the cave sediments (discussed below) are presented in Table 2.

Four of the 5 packrat middens recovered from Smith Creek Cave will be discussed. Radiocarbon dating of these middens indicates a time range from 11 650 ± 280 to 13 340 ± 430 yr B.P. (years before present, Table 2). Ladder Cave, a much smaller cave, is located immediately above Smith Creek Cave. We discuss 6 packrat middens from this cave, dating from 11 080 ± 115 to 27 280 ± 970 yr B.P. (Table 2). Two packrat middens from Council Hall Cave (Table 2) provided faunal remains of middle Holocene age (4220 ± 60 to 6120 ± 80 yr B.P.). Three middens reported from the Streamview locality date from the middle Holocene (6490 ± 190 yr B.P.), late glacial (11 010 ± 400 yr B.P.), and the end of the last full-glacial (17 350 ± 435 yr B.P.). Amy's Shelter is in the bottom of the canyon across the canyon from Smith Creek Cave. This site and Kachina Cave are included here to add the results of Miller's (1979) faunal study.

Smith Creek Cave stratigraphy.—The stratigraphy currently known from the

TABLE 2. Radiocarbon dated packrat middens and cave sediments from Smith Creek Canyon, Snake Range, Nevada (Thompson 1979, Thompson and Mead 1982). Associated plant material: A) Dung and/or unidentified plants; B) *Ephedra viridis*; C) *Juniperus communis*; D) *J. osteosperma*; E) *Picea engelmannii*; F) *Pinus flexilis*; G) *P. longaeva*; H) *P. monophylla*; I) *Artemisia* spp.; J) *Atriplex confertifolia*; K) *Cercocarpus intricatus*; L) *Chamaebatiaria millifolium*; M) *Chrysothamnus* sp.; N) *Foresellesia nevadensis*; O) *Ribes montigenum*; P) *Symphoricarpos* sp.; Q) *Rhus trilobata*.

Locality	Lab no.	Radiocarbon age (yr B.P.)	Material dated	Plant associates
Council Hall Cave (CHC)	1a Wk-157	6120 ± 80	D	BKNHQ
	1b Wk-158	4220 ± 60	D	BHKMQ
Ladder Cave (LC)	1 Wk-151	11 200 ± 200	G	DIKN
	2a WK-152	27 280 ± 970	P	BDINO
	2b A-2092	17 960 ± 110	A	GO
	3 Wk-154	13 230 ± 110	G	DILNO
	4 Wk-155	12 100 ± 150	G	IKNO
	6 Wk-156	11 080 ± 115	G	BDIKN
Smith Creek Cave (SCC)	1 Gx-5861	11 660 ± 245	A	FGKP
	3 Gx-5862	11 650 ± 280	G	MNP
	4 Gx-5863	12 235 ± 395	G	CIKN
	5 A-2094	13 340 ± 430	A	GILM
(Reddish-brown Silt: SCC Sed.)	Tx-1639	28 650 ± 760	(see text)	
Streamview Shelter (STV)	1 A-2095	11 010 ± 400	FG	INP
	2 Gx-5866	17 350 ± 435	G	CEJKN
	3 Gx-5867	6490 ± 190	D	BCGJK

northwestern sections of Smith Creek Cave was established from the excavation of Test Pits 2 and 3 (Bryan 1979*a*). The stratigraphic units established by Bryan will be followed in this report. Bryan recognized 3 stratigraphic "zones" in the rear of Smith Creek Cave, the lowest unit being the Cemented White Silt Zone. In the northwestern section of the cave, this unit was eroded away before the deposition of the second stratigraphic zone—the Reddish-brown Silt Zone. Bryan noted that the erosional disconformity between the Cemented White Silt Zone and the Reddish-brown Silt unit is near vertical. The reddish silt of the latter unit is believed to be of probable eolian deposition, although it is just as likely that water from a nearby ceiling conduit may have caused the erosion of the first stratigraphic unit and at least a partial deposition of the Reddish-brown Silt. This latter unit is very fossiliferous (partially a raptor accumulation) and is stained reddish-brown by the surrounding silt (dry 7/6 10YR, yellow; damp 5/8 7.5YR, strong brown, Munsell color; our observations). No organic remains, including charcoal, were observed in the Reddish-brown Silt by Bryan (1979*a*) or us. Permineralization has occurred with all of the red-stained bones (Miller 1979). Younger contaminating bones are white, not mineralized, and easily spotted.

Bryan (1979*a*) reported that "a sample of unidentified red-stained bone scrap [from Test Pit 2] yielded a collagen date of 28,650 ± 760 years B.P. (Tx-1639)." A discrepancy arises in that Valastro (1977) reported that the Tx-1639 ^{14}C date is from a charcoal sample from Test Pits 2 and 5; Test Pit 5 is at the mouth of the cave. We did not find charcoal in the unit in Test Pit 2. Because the red-stained bones in the Reddish-brown Silt in Test Pit 2 is permineralized with the loss of most bulk organic constituents (Miller 1979), we assume that the radiocarbon date from the unit is at best a very rough estimate of its true age and that the material dated was probably bone scraps, not charcoal. Further radiocarbon dating of this unit is in order.

Bryan indicated probable temporal correlations between the Reddish-brown Silt and the Laminated Pink Silt and Rubble Zone recognized in the excavation of the deposit at the mouth of the cave. Unlike the Reddish-brown Silt, this middle unit at the cave entrance rarely contains bones (Bryan 1979*a*). Although no radiometric dates were obtained from the Laminated Pink Silt and Rubble Zone, a ^{14}C date of 12 600 ± 170 B.P. (A-1565) was obtained at the lower boundary of the above unit—Bristlecone

TABLE 3. Wisconsinan and early Holocene fish, amphibians, and reptiles from Smith Creek Canyon. G) = previously reported by Goodrich (1965). B) = previously reported by Brattstrom (1958, 1976). 1) = now living within 50 miles; 2) = not living locally but elsewhere in Great Basin; 3) = not presently within the Great Basin; ? = age assignment in question.

	Present in Snake Range or nearby valley	Modern packrat midden	4000 to 6000 yr B.P.	11 000 to 12 000 yr B.P.	12 000 to 13 000 yr B.P.	13 000 to 14 000 yr B.P.	Smith Creek Cave: Reddish-brown Silt Zone ≥12 000–?≥28 000 yr B.P. (see text for discussion)	27 000 to 28 000 yr B.P.	Age unknown (Brattstrom 1976)
Fish									
Salmo clarki							X		
Gila atraria							X		
Amphibians									
Scaphiopus cf. *intermontanus*	X			X			X		
S. cf. *hammondi* (B)	3								X
Bufo boreas	2						X		
Bufo cf. *woodhousei*	1						X		
Bufo sp. (B)							X		
Rana sp.							X		
Reptiles									
Crotaphytus collaris	X						X		
Crotaphytus wislizeni	X						X		
Crotaphytus sp.							X		X
Sceloporus magister	2						X		
Sceloporus occidentalis or *undulatus*	X						X	X	
Sceloporus graciosus (B)	X						X		X
Sceloporus sp.							X		
Uta stansburiana (B)	X	X							X
Phrynosoma platyrhinos (B)	X						X		X
Phrynosoma douglassi	2					X	X	X	
Phrynosoma sp. (G)							X		
Cnemidophorus cf. *tigris*	X						X		
Coluber constrictor (G, B)	X						?		X
Masticophis flagellum (B)	2						?		X
Pituophis melanoleucus (G, B)	X						X		X
Lampropeltis getulus (G, B)	X						?		X
Lampropeltis pyromelana	X						X		
Lampropeltis triangulum	3						X		
Rhinocheilus lecontei	X	X					X		
Thamnophis sp. (G)							X		
Hypsiglena torquata (G, B)	X			X			X		X
Crotalus cf. *viridis* (G)	X						X		
Crotalus viridis (B)							X		X

Pine and Sheep Dung Zone (Bryan 1979*a*). Presumably this radiocarbon date provides a minimum age estimate for the Laminated Pink Silt and Rubble Zone and by correlation the Reddish-brown Silt unit.

The third depositional unit Bryan described from the rear of the cave is the Grey Silt, Rubble, and Dung Zone. Organic remains are very common within this unit. All bones incorporated in this uppermost unit are various shades of white without permineralization. Occasional mixing of the red-stained bones by bioturbation has occurred near the lower boundary of the unit. Although this unit has not been radiocarbon

dated, it certainly is younger than 10 000 yr B.P. and the upper portion probably is less than 3000 years old (Bryan 1979*a*).

Results

Table 3 is a chronological check-list of late Pleistocene and Holocene age fish, amphibians, and reptiles from Smith Creek Canyon. Many of these taxa have not been reported previously from the late Pleistocene of the Great Basin. Table 4 is an updated check-list of fossil mammals known from Smith Creek Canyon. Although previous reports have described the mammals (Harrington 1934, Stock 1936, Goodrich 1965, Miller 1979), this table shows their stratigraphic provenience, not adequately given before.

Following is an annotated list of the fossil fish, amphibians, reptiles, and mammals that we recovered from packrat middens and from one sedimentary layer (Reddish-brown Silt) in Smith Creek Cave. Abbreviations for the fossil localities are listed in Table 2. The number in parentheses refers to the quantity of that element. We follow the nomenclature and ordering, unless otherwise stated, of Smith (1978) for the fish, of Stebbins (1966) for the amphibians and reptiles, and of Jones et al. (1979) for the mammals.

Class Osteichthyes
Family Salmonidae
Salmo clarki (Cut-throat Trout)

Material.—SCC Sed.: R angular, R dentary, vertebrae (25).

Remarks.—The right angular resembles that of a small individual of the Great Basin, not of the Colorado River. The right dentary is of a specimen of approximately 100 mm in length. All the vertebrae are of small individuals. The skeletal elements were identified as *Salmo* rather than *Salvelinus malma* (Dolly Varden, the other trout in the Great Basin) because (1) the angle between the coronoid and post-dorsal process of the angular is near 90°, and (2) the dentary lacks the deep groove under the tooth platform. The small size of the specimens suggest that they were from a creek (Smith Creek?), not a lake (Lake Bonneville) (Gerald R. Smith identifications and personal communication 1981).

Distribution.—*Salmo clarki*, which occurred in Lake Bonneville during the Pleistocene, is the widespread trout of the Great Basin and Intermountain Region (Smith et al. 1968, Smith 1978).

Family Cyprinidae
Gila atraria (Utah Chub)

Material.—SCC Sed.: Basioccipital and vertebrae (3).

Remarks.—The basioccipital with a pharyngeal process has the shape and angles of *Gila atraria*, not *Richardsonius belteatus* (Redside Shiner), which has a less ovoid haemal canal and a less obtuse angle between the cranial part of the bone and its pharnygeal process. The basioccipital belonged to a fish about 110 mm long (Gerald R. Smith identification and personal communication 1981).

Distribution.—*Gila atraria* is native to the Bonneville and upper Snake River drainages and occurred in Lake Bonneville during the Pleistocene (Smith et al. 1968, Smith 1978).

Class Amphibia
Order Salientia
Family Pelobatidae
Scaphiopus cf. *intermontanus* (Great Basin Spadefoot Toad)

Material.—SCC 1: tibiofibula; SCC Sed.: tibiofibulae (13), radio-ulnae (3).

Remarks.—No comparative material was available for *Scaphiopus intermontanus* although we have an excellent series of the closely related *S. hammondi*.

Distribution.—Only this species of spadefoot toad presently occurs within woodlands and sagebrush areas in the Great Basin (as well as in the Snake Range); however, *S.* cf. *hammondi* has been identified from an unprovenienced level in Smith Creek Cave (Brattstrom 1976).

Family Bufonidae
Bufo boreas (Western Toad)

Material.—SCC Sed.: sacral vertebra, R ilium.

Distribution.—*Bufo boreas* presently occurs throughout most of the Great Basin except the drier eastern part along the Nevada-Utah border; it has not been found in the Snake Range.

Bufo cf. *woodhousei* (Woodhouse's Toad)

Material.—SCC Sed.: tibiofibula.

Remarks.—Martin (1973) used the ratio of the tibiofibula, minimum width relative to length, to differentiate species of *Bufo* (*B. boreas*: 690–760; *B. cognatus*: 840–1050; *B. hemiophrys*: 950–1160; *B. microscaphus*: 670–850; and *B. woodhousei*: 770–950). The ratio of the Smith Creek Cave sediment fossil is 1013 (1.84/18.16 mm × 10 000), being relatively stout and thick in the middle. Although our fossil could be identified as *B. cognatus* based upon the tibiofibula ratio, we refer our specimen to *B. woodhousei* because of its present closer distribution; *B. cognatus* does not live in the Great Basin. Additional fossils of *Bufo* are needed to refine our identification.

Distribution.—*Bufo woodhousei* presently does not inhabit much of the Great Basin; the western edge of its range is just north and east of the Snake Range.

Bufo sp. (toad)

Material.—SCC Sed.: tibiofibulae (3), radio-ulna.

Remarks.—We were unable to identify the fragmented fossils to species.

Family Ranidae
Rana sp. (frog)

Material.—SCC Sed.: tibiofibulae (4), coracoid, atlas.

Remarks.—We were unable to assign the specimens to species.

Distribution.—Presently *R. pretiosa* and *R. pipiens* occur within the Great Basin (Stebbins 1966).

Class Reptilia
Order Squamata
Suborder Sauria
Family Iguanidae
Crotaphytus collaris (Collared Lizard)

Material.—SCC Sed.: L dentaries (3), R dentary.

Remarks.—*C. collaris* and *C. wislizeni* can be separated from most other iguanid lizards by their larger size and their dental characters. The individual teeth of *C. collaris* are relatively wide anteroposteriorly as compared to those of *C. wislizeni*, the posterior teeth strongly tricuspid, the anterior tending toward blunt spikes, some with a slight posterior curve. In *C. wislizeni* the anterior three-quarters of the teeth are sharp, recurved simple cusps with only a few posterior teeth tricusped.

Distribution.—The Collared Lizard occurs throughout the Great Basin in a variety of mountain and rocky habitats.

Crotaphytus wislizeni (Leopard Lizard)

Material.—SCC Sed.: L dentaries (2), L maxillae (3), R dentaries (3), R maxillae (4).

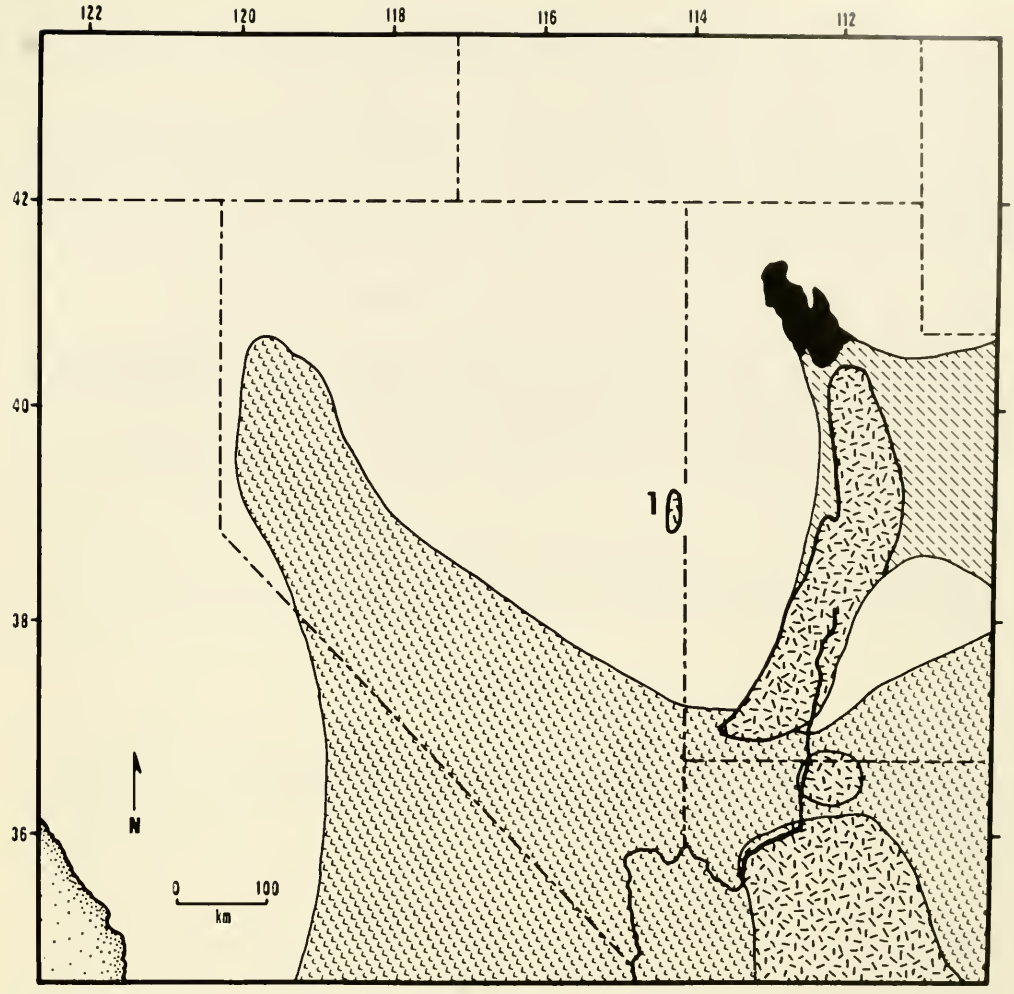

FIGURE 2. Present distributions of *Sceloporus magister* (L's), *Lampropeltis triangulum* (parallel lines), and *L. pyromelana* (mixed lines) (from Stebbins 1966). (1) Fossil localities and Snake Range. The distribution of *L. triangulum* overlaps the entire range of *L. pyromelana* only in Utah. The distribution of *S. magister* overlaps only the southern tip of both species of *Lampropeltis* in Utah and all of *L. pyromelana* in Arizona.

Remarks.—The distinguishing characters are listed under *C. collaris*.

Distribution.—Like the Collared Lizard, the Leopard Lizard occurs throughout the Great Basin, although usually in desertscrub communities on the finer alluvial habitats of the valleys.

Crotaphytus sp. (Collared or Leopard Lizard)

Material.—SCC Sed.: L dentaries (2), L maxillae (3), R dentaries (2), R maxilla.

Remarks.—We were unable to assign these elements to species.

Sceloporus magister (Desert Spiny Lizard)

Material.—SCC Sed.: L dentary.

Remarks.—The Desert Spiny Lizard can be differentiated from other sceloporine lizards of the Great Basin by its larger size.

Distribution.—The range of *S. magister* presently ends southwest of the Snake Range (Fig. 2). Although no other spiny lizards reach the size of *S. magister* in the Great Basin, other very similar sized species occur farther south in southern Arizona (*S. clarki* and *S. jarrovi*).

Sceloporus occidentalis or *undulatus* (Western or Eastern Fence Lizard)

Material.—LC 2a: epidermal scale; SCC Sed.: L dentaries (6), R dentaries (2), R maxillae (5), frontal.

Remarks.—There are no satisfactory dental criteria for separating the closely related *S. undulatus* and *S. occidentalis*; both species have larger races at their northern distribution. Since the latter species now lives within the Snake Range, we refer our fossils to it. The nearest population of *S. undulatus* is to the east in Utah. Both species possibly occurred within the mountain range in the late Pleistocene.

Sceloporus graciosus (Sagebrush Lizard)

Material.—SCC Sed.: R dentaries (2), frontal.

Remarks.—The skeletal elements of *S. graciosus* can be differentiated from those of other sceloporine lizards of the Great Basin by their distinctly smaller adult size and their slender pointed teeth with weakly developed secondary cusps.

Distribution.—*S. graciosus* now occurs throughout the Great Basin including the Snake Range.

Sceloporus sp. (spiny lizard)

Material.—SCC Sed.: L dentaries (2), L maxilla, R dentary, R maxillae (2).

Remarks.—We were unable to assign these elements to species.

Uta stansburiana (Sideblotched Lizard)

Material.—LC modern: L dentary.

Remarks.—The single element compared well with modern *Uta stansburiana*. The lizard presently lives in Smith Creek Canyon, and the only skeletal specimen recovered in our study came from a modern packrat midden.

Phrynosoma douglassi (Short-horned Lizard)

Material.—LC 2a: frontal; LC 3: L maxilla; SCC Sed.: L dentary, R maxillae (2), frontal.

Remarks.—The recovered dentary, maxillae, and frontals could not be distinguished from those of modern *P. douglassi*. In bone and dental characters of the frontal, dentary, and maxilla, *P. douglassi* are distinct from *P. platyrhinos* (Robinson and Van Devender 1973). *P. douglassii* has tall *Sceloporus*-like teeth with well-developed secondary cusps and a rounded bottom to the dentary. *P. platyrhinos* has short peg-like teeth with reduced secondary cusps.

Phrynosoma platyrhinos (Desert Horned Lizard)

Material.—SCC Sed.: L dentary.

Distribution.—Both *Phrynosoma platyrhinos* and *P. douglassi* live within the Great Basin today, the latter only at higher elevations on a few mountain ranges in northeastern Nevada (Stebbins 1966).

Family Teiidae

Cnemidophorus cf. *tigris* (Western Whiptail Lizard)

Material.—SCC Sed.: R dentaries (4).

Remarks.—We refer our specimens to *C.* cf. *tigris* because it is the only species of whiptail lizard now living within the interior Great Basin. Modern *C. tigris* and the fossils have very large dentaries. Other species of whiptail (e.g., *C. burti*) with dentaries of similar size now occur far south of the Great Basin.

Suborder Serpentes
Family Colubridae
Pituophis melanoleucus (Gopher Snake)

Material.—SCC Sed.: palatine, vertebrae (23).

Remarks.—The vertebrae of *Pituophis melanoleucus* are most similar to those of *Elaphe*. We used the criteria described by Auffenberg (1963) to differentiate the two species.

Distribution.—The Gopher Snake is very common throughout the Great Basin.

Lampropeltis pyromelana (Sonoran Mountain Kingsnake)

Material.—SCC Sed.: vertebrae (29).

Remarks.—The vertebrae of *Lampropeltis pyromelana* are typical of kingsnakes, with well-developed subcentral ridges. We differentiate *L. pyromelana* from *L. triangulum* by two criteria: (1) the cotyle and condyle are proportionally larger in *L. pyromelana* at all stages of growth, and (2) the accessory processes are fairly pointed on *L. pyromelana* whereas they are longer and globose (as viewed anteriorly) on *L. triangulum*. Both species have low neural spines unlike *L. getulus* or *Rhinocheilus lecontei*.

Distribution.—The Sonoran Mountain Kingsnake presently occurs only in a few relictual populations in the Great Basin including the Snake Range (Fig. 2). It commonly occurs in the central and southern Wasatch Mountains and the mountainous region farther south and west.

Lampropeltis triangulum (Milksnake)

Material.—SCC Sed.: vertebra.

Remarks.—The distinguishing criteria were discussed under *L. pyromelana*.

Distribution.—The Milksnake occurs on the eastern periphery of the Great Basin in the Wasatch Mountains and farther south in Utah but not as far west as the Snake Range (Fig. 2).

Rhinocheilus lecontei (Long-nosed Snake)

Material.—LC modern: vertebra; SCC Sed.: vertebrae (13)

Remarks.—The vertebrae of *Rhinocheilus* are quite characteristic and can readily be identified (Hill 1971, Van Devender and Mead 1978).

Distribution.—The Long-nosed Snake lives throughout the Great Basin except for the northwesternmost region.

Thamnophis sp. (garter snake)

Material.—SCC Sed.: vertebrae (3).

Remarks.—We were unable to assign the specimens to species.

Distribution.—Presently *T. elegans* (Wandering Garter Snake) lives within the Great Basin, including the Snake Range, and *T. sirtalis* (Common Garter Snake) borders parts of the basin (Stebbins 1966).

Hypsiglena torquata (Night Snake)

Material.—CHC 1b: vertebra; SCC Sed.: L dentary, vertebrae (36).

Remarks.—*H. torquata* has small generalized colubrid vertebrae, which are very similar to those of other small snakes such as *Sonora semianulata*. Identification criteria used here were those used by Van Devender and Mead (1978).

Distribution.—The Night Snake occurs over most of the Great Basin.

TABLE 4. Wisconsinan and Holocene mammals from Smith Creek Canyon, Nevada. The stratigraphic units discussed under Smith Creek Cave follow the nomenclature described by Bryan (1979*a*); their age assignments are discussed in this text. (*) = extinct taxa. (!) = this report represents the first reporting of this taxon from Smith Creek Canyon. (?) = We and/or others question the identification or age assignment. Systematic arrangement follows Jones et al. (1979).

		Smith Creek Canyon packrat middens. Age in yr B.P.									Smith Creek Cave sediments						Council Hall Cave	Amys Shelter	Kachina Cave
														Stratigraphic unit					
	Presently in Snake Range or immediate valley	4000–6000	6000–8000	8000–10 000	10 000–11 000	11 000–12 000	12 000–13 000	13 000–14 000	17 000–18 000	27 000–28 000	Goodrich 1965	Miller 1979	This report	Generalized—all levels	Reddish-brown Silt ≥12 000 yr B.P. (see text)	Grey Silt, Rubble and Dung ≤10 000 yr B.P. and other Holocene units	?≥23 000 yr B.P. Age not given (Miller 1979, Bryan 1979b)	Approximate (?) 1500–5000 yr B.P. (Miller 1979, Gruhn 1979)	Approximate (?) 600–2100 yr B.P. (Miller 1979, Tuohy 1979)
Soricidae	X											X			X			X	
Chiroptera	X											X	X	X	X		X		
Antrozous cf. *pallidus*	X										X			?	?	?			
Ochotona cf. *princeps*			X	X	X		X		X				X		X				
Ochotona princeps											X	X		X	X	X	X		
Sylvilagus idahoensis (!)	X						X												
Sylvilagus sp.	X											X	X	X	X	X	X	X	X
Lepus cf. *californicus*	X										X			?	?				
Lepus sp.	X										X	X	X	X	X	X	X	X	X
Eutamias minimus (!)	X												X		X				
E. cf. *umbrinus* (!)	X												X		X				
Eutamias sp.	X											X	X	X	X	X	X		X
Marmota flaviventris	X										X	X	X	X	X		X	X	
Ammospermophilus leucurus (!)	X									X			X		X				
Spermophilus cf. *townsendii*	X										?	X		X				X	
S. cf. *richardsonii* (!)						X	X						X						
S. cf. *beldingi* (!)	X								X				X						

TABLE 4. Continued.

	Presently in Snake Range or immediate valley	Smith Creek Canyon packrat middens. Age in yr B.P.									Smith Creek Cave sediments						Council Hall Cave	Amys Shelter	Ka-china Cave
														Stratigraphic unit					
		4000–6000	6000–8000	8000–10 000	10 000–11 000	11 000–12 000	12 000–13 000	13 000–14 000	17 000–18 000	27 000–28 000	Goodrich 1965	Miller 1979	This report	Generalized—all levels	Reddish-brown Silt ⩾12 000 yr B.P. (see text)	Grey Silt, Rubble and Dung ⩽10 000 yr B.P. and other Holocene units	?⩾23 000 yr B.P. Age not given (Miller 1979, Bryan 1979b)	Approximate (?) 1500–5000 yr B.P. (Miller 1979, Gruhn 1979)	Approximate (?) 600–2100 yr B.P. (Miller 1979, Tuohy 1979)
S. variegatus	X																X		
S. cf. *lateralis* (!)	X					X				X			X		X				
Spermophilus sp.	X									X	X		X	X	X		X		X
Thomomys cf. *talpoides*	?										X	X		X	X	X			
Thomomys sp.	X											X	X	X	X		X		X
Perognathus cf. *parvus*	X											X			X				
Perognathus sp.	X					X			X				X		X		X		X
Microdipodops cf. *megacephalus*												X			X				
Dipodomys cf. *ordii*	X											X			X				
Dipodomys sp.	X												X		X				X
Peromyscus sp.	X										X	X	X	X	X	X	X		X
Neotoma lepida	X	X	X						X		X	X	X	X	X		X	X	X
N. cinerea	X	X	X			X						X	X		X		X	X	X
Neotoma sp.	X	X	X	X	X	X	X	X	X	X			X		X				
N. lepida or *cinerea*	X	X	X										X		X				
Phenacomys cf. *intermedius* (!)													X		X				
Microtus cf. *montanus*	X										X			X	X	X			
M. cf. *longicaudus* (!)	X								X				X		X				
Microtus sp.	X						X		X			X	X	X	X		X	X	X
Erethizon dorsatum	X											X			X			X	

TABLE 4. Continued.

		Smith Creek Canyon packrat middens. Age in yr B.P.									Smith Creek Cave sediments						Council Hall Cave	Amys Shelter	Ka-china Cave
														Stratigraphic unit					
	Presently in Snake Range or immediate valley	4000–6000	6000–8000	8000–10 000	10 000–11 000	11 000–12 000	12 000–13 000	13 000–14 000	17 000–18 000	27 000–28 000	Goodrich 1965	Miller 1979	This report	Generalized—all levels	Reddish-brown Silt ≥12 000 yr B.P. (see text)	Grey Silt, Rubble and Dung ≤10 000 yr B.P. and other Holocene units	?≥23 000 yr B.P. Age not given (Miller 1979, Bryan 1979b)	Approximate (?) 1500–5000 yr B.P. (Miller 1979, Gruhn 1979)	Approximate (?) 600–2100 yr B.P. (Miller 1979, Tuohy 1979)
Canis cf. *latrans*	X											X			X		X	X	X
C. cf. *lupus*	?										X				?				
Vulpes vulpes	X											X			X				
V. velox												X			X				
Ursus sp.											X			?	?				
Bassariscus astutus	X										X			X	X				
Martes nobilis (*)												X			X				
Martes sp.											X				X				
Mustela erminea	X											X			X				
M. frenata	X											X				X			
M. vison												X			X				
Mustela sp.	X										X				X				
Taxidea taxus	X										X	X			X			X	X
Spilogale putorius	X												X		X				
Spilogale sp.	X										X	X			X	X			
Felis rufus	X										X	?		X	X			X	X
F. cf. *onca*											X				X				
F. onca												X			X				
F. concolor	X										X	?		X	X				X
?*F. atrox* (*)												X			?				
Equus sp. (Large) (*)											X	X			X				

TABLE 4. Continued.

	Presently in Snake Range or immediate valley	Smith Creek Canyon packrat middens. Age in yr B.P.									Smith Creek Cave sediments						Council Hall Cave	Amys Shelter	Kachina Cave
														Stratigraphic unit					
		4000–6000	6000–8000	8000–10 000	10 000–11 000	11 000–12 000	12 000–13 000	13 000–14 000	17 000–18 000	27 000–28 000	Goodrich 1965	Miller 1979	This report	Generalized—all levels	Reddish-brown Silt ≥12 000 yr B.P. (see text)	Grey Silt, Rubble and Dung ≤10 000 yr B.P. and other Holocene units	?≥23 000 yr B.P. Age not given (Miller 1979, Bryan 1979b)	Approximate (?) 1500–5000 yr B.P. (Miller 1979, Gruhn 1979)	Approximate (?) 600–2100 yr B.P. (Miller 1979, Tuohy 1979)
Equus sp. (Small) (*)											X	X			X				
Camelops sp. (*)											X	X			X				
?*Hemiauchenia* sp. (*)												X			X				
Cervus elaphus												X			X	?			
Odocoileus sp.	X										X			?	?		?	X	
Antilocapra americana	X											X		X	X	X	?		X
cf. *Antilocapra*	X																	X	
Antilocapridae	X										X				?				
?*Breameryx* sp. (*)												X			X				
?*Bison* sp.												X			X				X
Oreamnos harringtoni (*)											X	X			X				
Oreamnos americanus																	?		
cf. *Oreamnos*												X						X	
Ovis canadensis	X											X		X	X	X	X	X	X
?*Ovis aries*	?																?		
Ovis sp.	X										X			X	X	X			

Family Viperidae
Crotalus cf. *viridis* (Western Rattlesnake)

Material.—SCC Sed.: vertebrae (5)

Distribution.—We refer our specimens to *C. viridis* because they are from a medium-sized rattlesnake and this species presently inhabits the Great Basin. *C. mitchelli* is very similar but occurs no farther north than the Mohave Desert.

Class Mammalia
Order Chiroptera
Genus and species indeterminate

Material.—SCC Sed.: isolated teeth, mandible.

Remarks.—The isolated teeth and the fragment of a mandible did not allow generic identification.

Distribution.—Many species of bats occur in the Great Basin (Barbour and Davis 1969).

Order Lagomorpha
Family Ochotonidae
Ochotona cf. *princeps* (pika)

Material.—SCC 4: dung pellets (17), RM^1; SCC 5: dung pellets (2), RP^3; SCC Sed.: LP_3; STV 1: dung pellet; STV 2: dung pellets (>50); STV 3: dung pellets (3).

Remarks.—The RP^3 from SCC 5 is referred to *Ochotona,* but in view of its worn state, it could possibly be a *Sylvilagus idahoensis.* Miller (1979) reported that pika remains were recovered in all stratigraphic units in Smith Creek Cave; the youngest occurrence, however, cannot be determined. Pika also was recovered from Council Hall Cave; unfortunately, the remains (not described) were not reported in relation to the testpits, stratigraphy, or associated radiocarbon age (Miller 1979, Bryan 1979*b*). Small mammal bones (*Ochotona*?) occurred throughout the upper two meters (above a 23 900 ± 970 yr B.P. radiocarbon date, GaK-5100) of organic layers in Test Pit 2 (Bryan 1979*b*).

Two packrat middens in Smith Creek Cave and three middens in Streamview Shelter contained lagomorph dung pellets referable to *Ochotona* cf. *princeps* (Fig. 3). Dung pellets from each packrat midden were measured (length and width) and the measurements compared with those from samples from modern *Ochotona princeps, Sylvilagus idahoensis,* and *S. nuttallii.* The advantage of the preserved dung pellets from the packrat middens over the skeletal fragments from the cave sediments is that presumably *Ochotona* lived at the fossil site and was not brought there via a raptor stomach. Pika (skeletal remains) has been identified previously from mountain ranges outside its present distribution and from elevations below its current lower limit in ranges it now inhabits (Fig. 4; Grayson 1977, 1981, *in press a, b,* Miller 1979). To our knowledge, this is the first record of late Pleistocene age dung of *Ochotona* south of the permafrost in North America (Guthrie 1973). A more detailed account of the fossil *Ochotona* in the Great Basin is in progress.

Distribution.—Pika does not now live in the Snake Range or in any nearby mountains (Hall 1946, Hall and Kelson 1959), although it does inhabit the mountainous regions on the west, north, and east sides of the Great Basin (Fig. 4). Only *O. p. nevadensis* (Ruby Mountains region) and *O. p. tutelata* (Toquima Range and Desatoya Mountains) live in restricted relictual localities within the interior Great Basin.

Family Leporidae
Sylvilagus (=*Brachylagus*) *idahoensis* (Pygmy Rabbit)

Material.—SCC Sed.: M_3.

Remarks.—*S. idahoensis* has not been previously recorded from Smith Creek Canyon (Miller 1979). In the central Great Basin at Gatecliff Shelter, the Pygmy Rabbit

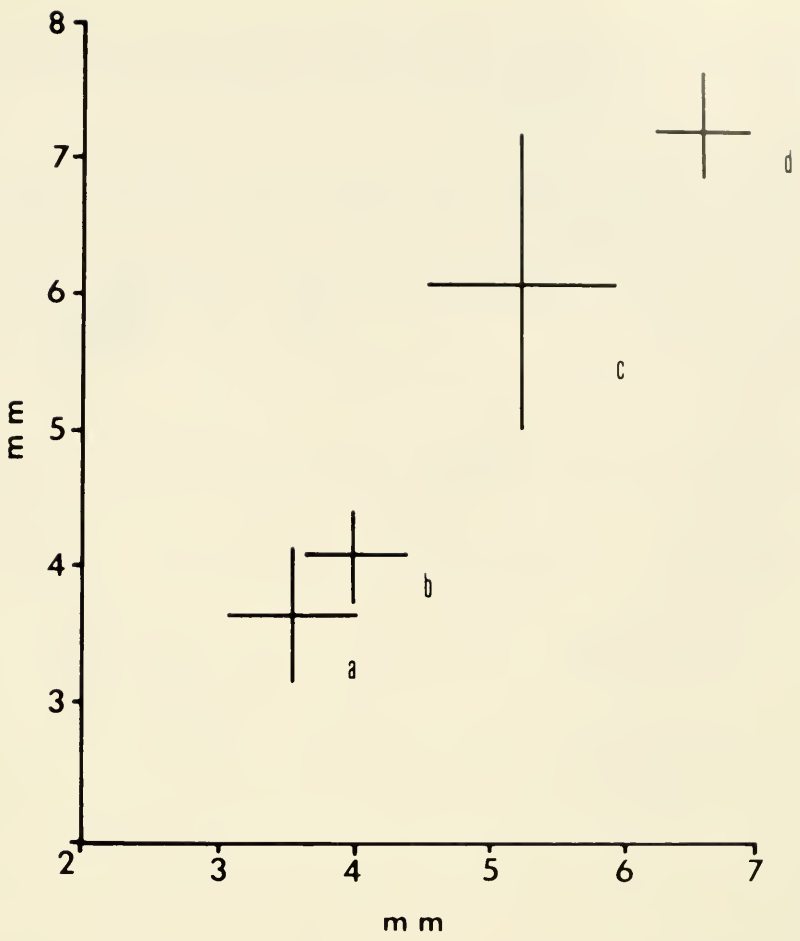

FIGURE 3. Measurements (width and length) of lagomorph dung pellets. (a) *Ochotona* cf. *princeps*, fossil, this report; (b) *O. princeps*, modern, California; (c) *Sylvilagus idahoensis*, modern, Nevada; (d) *S. nuttallii*, modern, Nevada.

was recovered throughout the deposit (Grayson *in press b*). North of the Great Basin, *S. idahoensis* is recorded in late Pleistocene context at Jaguar Cave (Guilday and Adams 1967), Wasden site (Owl Cave, Guilday 1969), and Moonshiner Cave (Anderson 1974). South of the Great Basin it is reported from Tule Springs, Nevada (Mawby 1967) and Isleta Cave, New Mexico (Harris 1977).

Distribution.—The Pygmy Rabbit presently occurs across the northern and east-central Great Basin (Hall 1946).

Sylvilagus sp. (rabbit)

Material.—SCC Sed.: RP^3.
Remarks.—The specimen could not be identified to species.

Lepus sp. (hare)

Material.—SCC Sed.: RM_3.
Remarks.—The specimen could not be identified to species.

FIGURE 4. Distribution of *Ochotona princeps* on isolated mountains within and bordering the Great Basin (from Hall 1946, Hall and Kelson 1959). (1) Fossil localities of Smith Creek Canyon and Garrison.

Order Rodentia
Family Sciuridae
Eutamias minimus (Least Chipmunk)

Material.—SCC Sed.: R mandible P_4M_{1-3}.

Remarks.—This is the smallest chipmunk in Nevada. Assignment of our specimens to this species was on the basis of size. Although the other species of *Eutamias* of the Great Basin are restricted to the vicinity of coniferous trees, *E. minimus* may live in sagebrush (*Artemisia tridentata*) at both high and low elevations (Hall 1946).

Eutamias cf. *umbrinus* (Uinta Chipmunk)

Material.—SCC Sed.: frontal.

Remarks.—Neither of the two species of *Eutamias* have been reported from Smith Creek Canyon (Miller 1979). Our specimen compared most favorably with modern *E. umbrinus*.

Distribution.—The Uinta Chipmunk is a medium-sized chipmunk that presently occurs in the Snake Range (Hall 1946).

Eutamias sp. (chipmunk)

Material.—SCC Sed.: LM_1 (2), RM_1, RM^1 (3), LM^3, RM^3.

Marmota flaviventris (Yellow-bellied Marmot)

Material.—SCC Sed.: LI.

Remarks.—Although we are assuming our specimen is *M. flaviventris*, the isolated incisor does not allow for specific identification. The Hoary Marmot, *Marmota caligata*, cannot be ruled out definitively based upon our specimen, though its occurrence in the Great Basin in the late Pleistocene seems unlikely.

Distribution.—*Marmota flaviventris* presently occurs in the Snake Range at elevations higher than Smith Creek Cave.

Ammospermophilus leucurus (White-tailed Antelope Squirrel)

Material.—LC 2a: frontal; SCC Sed.: L mandible M_{1-2}.

Remarks.—The White-tailed Antelope Squirrel has not previously been reported from Smith Creek Canyon (Miller 1979). Our specimens compare with modern representatives of *A. leucurus*.

Distribution.—*Ammospermophilus leucurus* presently lives in most of the Great Basin, including the area of the Snake Range (Hall 1946).

Spermophilus cf. *richardsonii* (Richardson's Ground Squirrel)

Material.—LC 1: RM^3; LC 4: LM_3.

Remarks.—*Spermophilus richardsonii* has not been recovered previously from Smith Creek Canyon, though it has been recorded from the more northern localities of Jaguar Cave (Guilday and Adams 1967) and Moonshiner Cave (Anderson 1974), Idaho. Both Davis (1939) and Hall (1946) have expressed the belief that *S. richardsonii* must have occupied a much wider range over an ecological area now filled by *S. beldingi* and *S. armatus*. On the basis of the Smith Creek Canyon fossils of *S.* cf. *richardsonii*, we concur with them. Our two specimens compared most favorably with modern *S. richardsonii*.

Distribution.—Richardson's Ground Squirrel does not occur presently in the Snake Range. The present distribution of *S. r. nevadensis* in the Great Basin is centered in the Independence Mountains of northern Nevada, and it occurs no farther south than the Roberts Mountains (Hall 1946).

Spermophilus cf. *beldingi* (Belding's Ground Squirrel)

Material.—LC 2b: L maxilla M^1.

Remarks.—*Spermophilus beldingi* has not been reported previously from Smith Creek Canyon, and the only other published fossil or subfossil record for Belding's Ground Squirrel in the Great Basin is from Stratum 3 at Gatecliff Shelter (Grayson *in press b*). Our single specimen compared most favorably with modern *S. beldingi*.

Distribution.—*Spermophilus beldingi* is ecologically and physically very similar to *S. richardsonii*. Belding's Ground Squirrel presently does not occur in the Snake Range or in any immediate mountain range. Its present distribution centers in the northern Sierra Nevada and in the higher mountains of north central and northern Great Basin, though it occurs farther south than *S. richardsonii*, down to the Toquima Range (Hall 1946).

Spermophilus cf. *lateralis* (Golden-mantled Ground Squirrel)

Material.—LC modern: RM_1; LC 2a: L maxilla M^{1-3}, L mandible M_{1-3}; SCC 1: R mandible P_4M_1; SCC Sed.: R mandible M_{1-2}, RM_3, LM^1, RM_{1-2}.

Remarks.—Although *S. lateralis* was not previously reported from Smith Creek Canyon (Miller 1979), it is fairly widespread in the Smith Creek Canyon fossil localities

and apparently was common in the canyon throughout most of the late Pleistocene. Although we have found this to be the most common species of *Spermophilus*, Miller (1979) considered that *S.* cf. *townsendii* was the most prevalent in the Smith Creek Cave record. Miller (1979) stated that Goodrich (1965) referred his specimens from Smith Creek Cave to *S.* cf. *townsendii*; although he considered that species, he did not definitely refer his specimens there. However, the presence of Townsend's Ground Squirrel in Smith Creek Canyon in the late Pleistocene seems plausible.

Spermophilus sp. (ground squirrel)

Material.—LC 2b: RM_1; SCC Sed.: P^4 (3), RM_3, RM^3.

Family Geomyidae
Thomomys sp. (pocket gopher)

Material.—SCC Sed.: LM^1.
Remarks.—We were unable to assign our single specimen to a species.

Family Heteromyidae
Perognathus sp. (pocket mouse)

Material.—SCC 1: L mandible P_4 (3), R mandible, R maxilla M^1; SCC Sed.: L mandible, R maxilla M^1 (2); STV 2: L maxilla (2), R maxilla.
Remarks.—We were unable to assign these specimens to species.

Dipodomys sp. (kangaroo rat)

Material.—SCC Sed.: LP^4.
Remarks.—We were unable to assign this specimen to species.

Family Cricetidae
cf. *Peromyscus* (white-footed mouse)

Material.—CHC 1b: RM^{1-2}; SCC 1: LM^1; SCC Sed.: LM^1, $RM^{1,3}$; STV 2: LM_1, RM^{1-2}; STV 3: LM_{1-2}.
Remarks.—We have not identified these specimens to species because we do not have available a sufficient comparative collection of *Reithrodontomys* and *Peromyscus* from Nevada. Presently *Reithrodontomys megalotis, Peromyscus eremicus, P. crinitus, P. maniculatus, P. boylii*, and *P. truei* live in or near the Great Basin. Previous work at Smith Creek Cave has produced specimens assigned to *Peromyscus* sp., but *Reithrodontomys* and *Onychomys* have not been identified from the fossil localities in Smith Creek Canyon, though they very well may be included.

Neotoma lepida (Desert Packrat)

Material.—CHC 1a: LM^{1-2}; CHC 1b: LM_1 (2); SCC Sed.: LM_1 (2), RM_1 (2), RM^1 (3), LM^1 (8); STV 2: RM^2.

Neotoma cinerea (Bushy-tailed Packrat)

Material.—CHC 1a: LM^1, RM^1 (2); CHC 1b: LM_1, LM^1; SCC 1: lower leg assemblage with hide; SCC Sed.: RM_1, RM^1 (7).
Remarks.—*Neotoma lepida* and *N. cinerea* are found living in Smith Creek Canyon. Their middens, both modern and fossil, can be found throughout the Great Basin. The excellent preservation and the advantages of having a packrat midden are illustrated by the partial mummy of the hind quarters of the Bushy-tailed Packrat (ca. 11 600 yr B.P.). Molars of *N. cinerea* are generally larger than those of *N. lepida*.

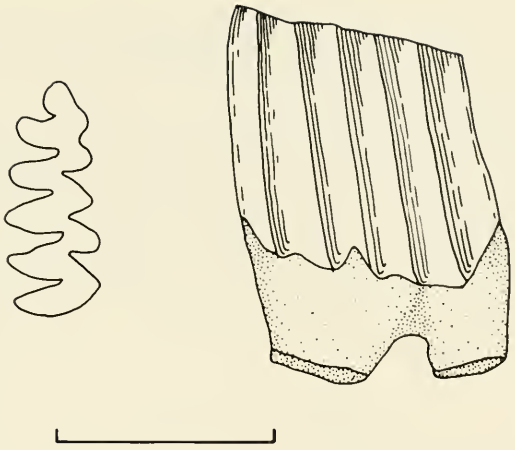

FIGURE 5. Occlusial (left) and lingual (right) views of the *Phenacomys* cf. *intermedius* RM_1 from Smith Creek Cave. Bar = 2 mm.

Neotoma lepida or *cinerea* (Desert or Bushy-tailed Packrat)

Material.—CHC 1a: RM^2; CHC 1b: L&RM^2 (5), LM_2 (2), M^3 (2), M_3 (2); SCC Sed.: LM_1 (2), RM_1 (2), L&RM_2 (17), L&RM^2 (8), M^3 (8), M_3 (8).

Neotoma sp. (packrat)

Material.—SCC Sed.: M_3; STV 2: M fragment.

Phenacomys cf. *intermedius* (Heather Vole)

Material.—SCC Sed.: RM_1.

Remarks.—Only one specimen was identifiable as *Phenacomys* cf. *intermedius*. Criteria for identification were the presence of tooth roots, lack of cementum, and distinctive occlusal pattern (Fig. 5; Guilday and Parmalee 1972). The isolated molar does not allow for specific identification.

Distribution.—The Heather Vole presently does not live in the Great Basin (Hall 1946). Our specimen from Smith Creek Cave is the first reported late Pleistocene *Phenacomys* from the Great Basin. Grayson (1981) has recovered a specimen from Gatecliff Shelter dating approximately 5300 yr B.P., which illustrates the middle Holocene survival of this presently extirpated mammal.

Microtus cf. *longicaudus* (Long-tailed Vole)

Material.—SCC Sed.: RM_1 (7), LM_1 (8), R mandible: STV 2: LM_3.

Remarks.—Our fossil specimens appear most similar to the Long-tailed Vole, although we find it difficult to differentiate *M. longicaudus* from *M. montanus*. Of the 15 fossil M_1's examined, 14 had five closed alternating triangles, 1 had six triangles. Only *M. montanus* has been reported from Smith Creek Cave (Goodrich 1965, Miller 1979). Goodrich compared his fossils with *M. californicus*, *M. montanus*, *M. townsendii*, *M. oregoni*, and *M. pennsylvanicus*; *M. longicaudus* was not compared.

Distribution.—*Microtus montanus* and *M. longicaudus* are the only species of meadow vole in Nevada (Hall 1946). Normally, *M. montanus* is found in the valleys and *M. longicaudus* in the mountains.

Microtus sp. (meadow vole)

Material.—LC 2b: RM_{1-2}; SCC 4: RM_1; SCC Sed.: LM^1 (3), RM^1 (3), LM^2 (4), LM_2 (4), RM_3 (2), LM_3 (2), RM^3.

Order Carnivora
Family Mustelidae
Spilogale putorius (Spotted Skunk)

Material.—SCC Sed.: L mandible $C_1P_{3-4}M_{1-2}$.

Remarks.—This is the only place where we disagree with the classification of Jones et al. (1979). We follow Kurten and Anderson (1980) and group the Western Spotted Skunk (*Spilogale gracilis*) with the Eastern Spotted Skunk (*S. putorius*). Our specimen from Smith Creek Cave has an alveolar length (anterior edge of C_1 to posterior edge of M_2) of 19.0 mm and an occlusial length of the M_2 of 2.1 mm. These measurements compare well with two modern specimens of *S. putorius* from the Ruby Mountains, Elko and White Pine Counties, Nevada.

Distribution.—The Spotted Skunk is common throughout the Great Basin.

Order Artiodactyla
Genus and species indeterminate

Material.—CHC 1a: dung pellets (15); SCC 1: keratinous hoof fragment; SCC Sed.: 1 fragment.

Remarks.—Because of fragmented state of preservation, we were unable to identify further these specimens.

Discussion and Summary

We report here the occurrence of 2 fish, 4 anurans, 9 lizards, 8 snakes, and 17 small mammals. This assemblage adds 15 amphibians and reptiles and 7 mammals to the approximately 46 animals previously known from the late Pleistocene and early Holocene of Smith Creek Canyon (Goodrich 1965, Miller 1979). Over half of the large herbivores (*Equus* spp., *Camelops* sp., ?*Hemiauchenia* sp., *Oreamnos harringtoni*, and ?*Breameryx* sp.) and the two carnivores (*Martes nobilis* and ?*Felis atrox*) reported from Smith Creek Canyon are extinct (Miller 1979). Our data add no large herbivore or carnivore species to the local fauna. Of the extant species from the fossil sites, 16 are not recorded from the Snake Range or in the immediate valleys (*Bufo boreas, Sceloporus magister, Phrynosoma douglassi, Lampropeltis triangulum, Masticophis flagellum, Ochotona princeps, Spermophilus* cf. *richardsonii, S.* cf. *beldingi, Phenacomys* cf. *intermedius, Vulpes velox, Ursus* sp., *Mustela vison, Martes* sp., *Felis onca, Cervus elaphus*, and ?*Bison* sp.).

Few large herbivores presently occur in the Snake Range. *Ovis canadensis* was reintroduced in the middle 1900s. The historic distributions of *Cervus elaphus* and *Bison bison* in the eastern Great Basin are not well known, though *Cervus* has been sighted in White Pine County (Hall 1946). The late Pleistocene occurrences of *Camelops* sp., ?*Hemiauchenia* sp., *Cervus elaphus, Odocoileus* sp., *Equus* (both large and small species), ?*Breameryx* sp., *Antilocapra americana, Oreamnos harringtoni, Ovis canadensis*, and ?*Bison* in Smith Creek Canyon are fairly well documented, although the exact timing (late or middle Wisconsinan) of these occurrences is not understood and is discussed below. We question the tentative identification of *Oreamnos americanus* reported from Council Hall Cave (Miller 1979). Although the estimated age is not reported for the modern mountain goat specimen (it is not known historically from the Great Basin), we speculate that the record, if *Oreamnos*, is of the extinct *Oreamnos harringtoni*.

If our reconstruction of the Smith Creek Canyon fauna-flora assemblage is correct, during the late Pleistocene, montane glaciers on Mount Moriah (3673 m elevation) moved down into the upper reaches of Smith Creek Canyon to an estimated elevation of 2900 m (Drews 1958). This was also a time when an open forest with *Pinus longaeva, P. flexilis*, and *Picea engelmannii* was present on the coarse talus and rock outcrops of the limestone entrance region of the canyon. Alluvial substrates in the canyon bottom probably supported a mosaic of *Artemisia* spp., shrubs, meadows, and riparian

TABLE 5. Fauna from two packrat middens on a rock outcrop in the middle of Snake Valley (1640 m elevation), near Garrison, Utah. (D) = dung. (B) = bone or tooth.

	Garrison No. 1 12 230 ± 180 yr B.P.	Garrison No. 2 13 480 ± 250 yr B.P.
Gastropoda		shell
Osteichthyes		B
Aves		B
Sorex sp.		B
Ochotona cf. *princeps*	D	B, D
Sylvilagus idahoensis	B	B
Thomomys sp.		B
Spermophilus sp.		B
cf. *Peromyscus*		B
Neotoma sp.	D	B, D
Microtus sp.	B	B
Camelops cf. *hesternus*		B
Ovis or *Odocoileus*		D

elements. This canyon bottom habitat and possibly the canyon slopes could have supported much of the fauna (e.g., *Phenacomys* and *Microtus*) recovered from the three caves and the rockshelters. *Ochotona* cf. *princeps* probably occurred on all suitable talus slopes throughout the unglaciated portions of the canyon from the creek level at Streamview to Smith Creek Cave.

Smith Creek Canyon empties into the broad Snake Valley to the east. During part of the late Wisconsinan a western arm of Lake Bonneville filled this valley to an elevation of 1580 m (Mifflin and Wheat 1979). This high lake stand was only 4 km from the entrance of Smith Creek Canyon. The late Pleistocene vegetation of the Snake Valley in the area above the lake level is poorly known.

Thirty km south of Smith Creek Canyon but still within Snake Valley, we recovered packrat middens from a rocky outcrop in the center of the valley (near the town of Garrison, Utah, 10 km east of the Snake Range, the closest mountain mass). The late Pleistocene age fauna-flora assemblage from the packrat middens is presumably an indication of the type of habitat above the pluvial lake level but below the mountain masses. The isolated rock outcrop provided a suitable habitat for limber pine and pika (Table 5; Thompson and Mead 1982). Adjacent areas appear to have been a shrub community, with some nearby areas of meadow. Megafauna of the valley consisted of at least *Camelops* cf. *hesternus* and *Ovis* or *Odocoileus* (Table 5). The Rancholabrean age fauna of Snake Valley is not well known. A cave acting as a natural trap has produced the skull of a wolverine (*Gulo gulo*), though unfortunately the age of the animal is not known (Barker 1976).

The density of the shrub communities below the mountain mass but above the lake level cannot be determined with certainty. The recovery of *Sylvilagus idahoensis* implies that at least some areas were fairly dense with tall stands of *Artemisia* spp. (Hall 1946). Conversely, the recovery of *Crotaphytus wislizeni* and *Phrynosoma platyrhinos* imply areas of relatively open to sparse habitat, possibly exposed playa adjacent to the lake.

Most of the fauna reported here (Tables 3 and 4) come from the inadequately dated Reddish-brown Silt Zone in Smith Creek Cave. We have already mentioned that the accuracy of the single radiocarbon date on bone fragments from the unit (ca. 28 000 yr B.P.) is suspect. The minimum age this unit could be is approximately 12 000 yr B.P., assuming the stratigraphic associations described by Bryan (1979*a*) are correct. Equally plausible is that the unit may date from the late Wisconsinan full glacial (ca. 18 000 to 22 000 yr B.P.) or even middle Wisconsinan (≥30 000 yr B.P.). The temporal depth of this unit also is not known. Because of these drawbacks we cannot definitely state when or what the faunal associations were in the late Pleistocene of Smith Creek

Canyon. We can state, however, that at least these taxa were in the canyon during the late Wisconsinan. This becomes important when considering the species such as *Ochotona, Phenacomys,* and other locally extirpated animals.

Tanner (1978) has stated that most of the present Great Basin Desert reptiles have extended their ranges into the Great Basin as post-Pleistocene introductions from a Pleistocene refugium of the southern deserts (Chihuahua, Coahuila, Sonora; Ballinger and Tinkle 1972). The late Wisconsinan records of *Crotaphytus wislizeni, Phrynosoma platyrhinos, Sceloporus magister, Hypsiglena torquata* and *Rhinocheilus lecontei* in the Smith Creek Canyon fauna presented here does not support Tanner's hypothesis. If the fauna from the Reddish-brown Silt Zone in Smith Creek Cave is of approximately 12 000 to 22 000 yr B.P. or even >30 000 yr B.P., then many of the lizards and snakes presently inhabiting the eastern Great Basin are not post-Pleistocene invaders. The important fact is that desert elements in the modern fauna were already in the Great Basin prior to the end of the late Wisconsinan. These results call for reconsideration of current biogeographical hypotheses on the evolution of the Great Basin Desert fauna.

At some time in the late Pleistocene and early Holocene, some of the amphibians, reptiles, and mammals found in the Snake Range and Snake Valley either adjusted their distributions or became extinct. Martin (1967) has previously expressed his model that Early Man exterminated the megafauna of North America. The amphibians, reptiles, and small mammals adapted individually to the climatic changes, however minor or major, of the late Pleistocene and Holocene.

Brown (1971, 1978) and Grayson (1981, *in press a, b*) have theorized that local extirpations in the Great Basin of an assemblage of small mammals on a mountain range are related to the size of the animal population and the mass of the mountain. In the case of the Snake Range (emphasizing Smith Creek Canyon) certain animal species became extirpated (*Sceloporus magister, Phenacomys* cf. *intermedius, Ochotona* cf. *princeps,* and others) while additional species developed relictual populations, inhabitants of a boreal island in a sea of sagebrush (e.g., *Lampropeltis pyromelana* and *Marmota flaviventris*). The smaller mammals, at least *Ochotona* and *Phenacomys,* lingered on into the early Holocene (Grayson 1981; this report). The *Ochotona* cf. *princeps* remains reported here indicate that suitable habitat and climate occurred in the Snake Valley at least until ca. 12 000 yr B.P. and in Smith Creek Canyon until ca. 6500 yr B.P. (Thompson and Mead 1982). Similar extralocal occurrences of *Ochotona* are documented as late as 7000 yr B.P. in eastern Oregon (Grayson 1981, *in press*). Grayson has argued that the timing of extinction of these relictual small mammal (and possibly some amphibian and reptile) populations was in large part determined by the size and distribution of habitat islands and by the size of the species population on the given habitat island. It is also possible that the mid-Holocene period of warmer-than-present temperatures, seen in the elevational raising of upper treeline on the Snake Range and elsewhere in the Great Basin (LaMarche 1973, LaMarche and Mooney 1972) may have reduced the size of montane habitat islands and accelerated the rate of extinction of animal populations.

The faunal account presented here is the first detailed account of amphibians and reptiles from late Pleistocene and early Holocene age deposits in the interior Great Basin; in addition, the assemblage has provided additional data on mammalian species. The *Phenacomys* cf. *intermedius* reported here is the first late Pleistocene record of the genus in the Great Basin. Because some of the fauna (especially *Ochotona*) was recovered from packrat middens, it is associated directly with a reconstruction of the local flora based on plant macrofossils. To our knowledge, similar plant and animal associations have not been pursued in this detail for the Great Basin.

The research in Smith Creek Canyon over the last 50 years has illustrated the wealth of information, mainly faunal, available in dry cave deposits of the Great Basin. With the recent surge of packrat midden analyses in Smith Creek Canyon, a whole new aspect of late Pleistocene and Holocene community reconstruction has emerged. Faunal assemblages can now be found in and associated temporally with the wealth of flora data recoverable from packrat middens.

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Literature Cited

Anderson, Elaine. 1974. A survey of the late Pleistocene and Holocene mammal fauna of Wyoming. Pages 78–87 *in* Michael Wilson (editor). Applied geology and archaeology: the Holocene history of Wyoming. Report of Investigation No. 10, Geological Survey Wyoming, Laramie, Wyoming.

Auffenberg, Walter. 1963. The fossil snakes of Florida. Tulane Studies in Zoology 10:131–216.

Ballinger, Royce E., and Donald W. Tinkle. 1968. A new species of *Uta* (Sauria: Iguanidae) from Salsipuedes Island, Gulf of California, Mexico. Occasional Papers of the Museum of Zoology, University of Michigan No. 656.

Barbour, Roger W., and Wayne H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington, Kentucky, USA.

Barker, Marcus S. 1976. The wolverine (*Gulo luscus*) in Nevada. Southwestern Naturalist 21:133.

Brattstrom, Bayard H. 1958. Additions to the Pleistocene herpetofauna of Nevada. Herpetologica 14:36.

———. 1976. A Pleistocene herpetofauna from Smith Creek Cave, Nevada. Southern California Academy of Science Bulletin 75:283–284.

Brown, James H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–477.

———. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Pages 209–227 *in* K. T. Harper and James L. Reveal (editors). Intermountain Biogeography: a symposium. Great Basin Naturalist Memoirs No. 2.

Bryan, Alan L. 1979*a*. Smith Creek Cave. Pages 262–251 *in* Donald R. Tuohy and Doris L. Rendall (editors). The archaeology of Smith Creek Canyon, eastern Nevada. Nevada State Museum, Anthropological Papers No. 17.

———. 1979*b*. Council Hall Cave. Pages 254–268 *in* Donald R. Tuohy and Doris L. Rendall (editors). The archaeology of Smith Creek Canyon, eastern Nevada. Nevada State Museum, Anthropological Papers No. 17.

Davis, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Limited. Caldwell, Idaho, USA.

Drewes, Harald. 1958. Structural geology of the southern Snake Range, Nevada. Geological Society of America Bulletin 69:221–240.

Goodrich, Robert B. 1965. The Quaternary mammalian microfaunal assemblage of Smith Creek Cave, Nevada. Master's thesis. California State University at Los Angeles, California.

Grayson, Donald K. 1977. On the holocene history of some northern Great Basin lagomorphs. Journal of Mammalogy 58:507–513.

———. 1981. A mid-Holocene record for the heather vole, *Phenacomys* cf. *intermedius*, in the central Great Basin and its biogeographic significance. Journal of Mammalogy 61:115–121.

———. *in press a*. Notes on the history of Great Basin mammals during the past 15,000 years. *In* D. B. Madsen and J. F. O'Connell (editors). Desert Varnish: a review of anthropological archaeology in the Great Basin. Society for American Archaeology Memoir 2.

———. *in press b*. The paleontology of Gatecliff Shelter small mammals. *In* D. H. Thomas (editor). The archaeology of Gatecliff Shelter and Monitor Valley. American Museum of Natural History Anthropological Papers, New York, New York.

Gruhn, Ruth. 1979. Excavation in Amy's Shelter, eastern Nevada. Pages 90–160 *in* Donald R. Tuohy and Doris L. Rendall (editors). The archaeology of Smith Creek Canyon, eastern Nevada. Nevada State Museum, Anthropological Papers No. 17.

Guilday, John E. 1969. Small mammal remains from the Wasden site (Owl Cave), Bonneville County, Idaho. Tebiwa 12:47–57.

———, and Eleanor K. Adams. 1967. Small mammal remains from Jaguar Cave, Lemhi County, Idaho. Tebiwa 10:26–36.

———, and Paul W. Parmalee. 1972. Quaternary periglacial records of voles of the genus *Phenacomys* Merriam (Cricetidae: Rodentia). Quaternary Research 2:170–175.

Guthrie, R. D. 1973. Mummified pika (*Ochotona*) carcass and dung pellets from Pleistocene deposits in interior Alaska. Journal of Mammalogy 54:970–971.

Hall, E. Raymond. 1946. Mammals of Nevada. University of California Press, Berkeley, California, USA.

———, and Keith R. Kelson. 1959. The mammals of North America. The Ronald Press Company. New York, New York, USA.

Harrington, Mark R. 1934. American horses and ancient men in Nevada. The Masterkey, Southwest Museum Publication 8:165–169.

Harris, Arthur H. 1977. Wisconsin age environments in the northern Chihuahuan Desert: evidence from the higher vertebrates. Pages 23–51 *in* Roland H. Wauer and David H. Riskind (editors). Transactions of the symposium on the biological resources of the Chihuahuan Desert region United States and Mexico. National Park Service Transactions and Proceedings Series No. 3.

Hill, William H. 1971. Pleistocene snakes from a cave in Kendall County, Texas. The Texas Journal of Science 22:209–216.

Howard, Hildegarde. 1935. A new species of eagle from a Quaternary cave deposit in eastern Nevada. Condor 37:206–209.

———. 1952. The prehistoric avifauna of Smith Creek Cave, Nevada. Bulletin of the Southern California Academy of Sciences 51:50–54.

Jones, J. Knox, Dilford C. Carter, and Hugh H. Genoways. 1979. Revised checklist of North American mammals north of Mexico, 1979. Occasional Papers the Museum, Texas Tech University No. 62.

Kurtén, Björn, and Elaine Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.

LaMarche, Valamore C. 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. Quaternary Research 3:632–660.

———, and H. A. Mooney. 1972. Recent climatic change and development of the bristlecone pine (*P. longaeva* Bailey) krummholz zone, Mt. Washington, Nevada. Arctic and Alpine Research 4:61–72.

Martin, Robert F. 1973. Osteology of North American *Bufo*: The *Americanus*, *Cognatus*, and *Boreas* species groups. Herpetologica 29:375–387.

Martin, Paul S. 1967. Prehistoric overkill. Pages 75–120 *in* Paul S. Martin and Herbert E. Wright (editors). Pleistocene extinctions, the search for a cause. Yale University Press, New Haven, Connecticut, USA.

Mawby, John E. 1967. Fossil vertebrates of the Tule Springs site, Nevada. Pages 105–128 *in* H. M. Wormington and Dorothy Ellis (editors). Pleistocene studies in southern Nevada. Nevada State Museum, Anthropological Papers No. 13.

Mifflin, M. D., and M. M. Wheat. 1979. Pluvial lakes and estimated fluvial climates of Nevada. Nevada Bureau of Mines and Geology Bulletin 94.

Miller, Susanne J. 1979. The archaeological fauna of four sites in Smith Creek Canyon. Pages 271–329 *in* Donald R. Tuohy and Doris L. Rendall (editors). The archaeology of Smith Creek Canyon, eastern Nevada. Nevada State Museum, Anthropological Papers No. 17.

Robinson, Michael D., and Thomas R. Van Devender. 1973. Miocene lizards from Wyoming and Nebraska. Copeia 1973:698–704.

Smith, Gerald R. 1978. Biogeography of intermountain fishes. Pages 17–42 *in* K. T. Harper and James L. Reveal (editors). Intermountain Biogeography: a symposium. Great Basin Naturalist Memoirs No. 2.

———, W. L. Stokes, and K. F. Horn. 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968:807–816.

Stebbins, Robert C. 1966. A field guide to western reptiles and amphibians. The Peterson field guide series, Houghton Mifflin Company, Boston, Massachusetts, USA.

Stock, Chester. 1936. A new mountain goat from the Quaternary of Smith Creek Cave, Nevada. Bulletin of the Southern California Academy of Sciences 35:149–153.

Tanner, Wilmer W. 1978. Zoogeography of reptiles and amphibians in the Intermountain Region. Pages 42–53 *in* K. T. Harper and James L. Reveal (editors). Intermountain Biogeography: a symposium. Great Basin Naturalist Memoirs No. 2.

Thompson, Robert S. 1979. Late Pleistocene and Holocene packrat middens from Smith Creek Canyon, White Pine County, Nevada. Pages 361–380 *in* Donald R. Tuohy and Doris L. Rendall (editors). The archaeology of Smith Creek Canyon, eastern Nevada. Nevada State Museum, Anthropological Papers No. 17.

———, and Jim I. Mead. 1982. Late Quaternary environments and biogeography in the Great Basin. Quaternary Research 17:39–55.

Valastro, S., E. Mott Davis, and Alejandra G. Varela. 1977. University of Texas at Austin radiocarbon dates XI. Radiocarbon 19:280–325.

Van Devender, Thomas R., and Jim I. Mead. 1978. Early Holocene and late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. Copeia 1978:464–475.

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Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of Central Texas

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Abstract. The Lower Albian carbonate rocks of the Glen Rose Limestone of Central Texas contain a diverse decapod fauna dominated by *Protocallianassa* species with 10 other taxa represented by fewer specimens. The fauna consists of *Protocallianassa* species, *P. klofi,* new species, *Pagurus banderensis* Rathbun 1935, *Roemerus robustus,* new genus and species, *Palaeodromites naglei,* new species, *Diaulax roddai,* new species, *Hillius youngi,* new genus and species, *Dioratiopus scotti,* new species, *Pseudonecrocarcinus stenzeli,* new species, *Prehepatus hodgesi,* new species, and *Torynomma? densus,* new species.

Introduction

The remains of fossil decapods have been among the most rarely reported fossils in the Glen Rose Limestone of Central Texas. Rathbun (1935:35) described *Pagurus banderensis* from a single fragmental specimen. Stenzel (1945:435) revised that description on the basis of several additional specimens and mentioned that other decapods were associated with the *P. banderensis* remains described by him. "Among the other chelae found by Mr. Watkins at the same locality there are some which obviously can have nothing to do with *Pagurus,* because they belong to other well-established and unrelated genera such as *Callianassa*" (Stenzel 1945:437).

The fauna described here is important because it testifies to the presence, abundance, and diversity of the decapod fauna of the Glen Rose Limestone. This fauna adds to our knowledge of the Early Cretaceous decapod fauna of North America. A diverse fauna of Late Albian age has been described by Rathbun (1935).

The Glen Rose Limestone

The Glen Rose Limestone is composed of beds of limestone that are resistant to weathering alternating with less resistant marls, giving rise to a characteristic stair-step topography (Fig. 1). The presence of mud cracks, bored bedding planes, bedding planes with encrusting oysters, algal mat laminations, ripple marks, dinosaur trailways, and plant debris is evidence for supratidal, intertidal, or shallow subtidal conditions. Beds of lime muds containing echinoids, miliolid foraminifera, infaunal pelecypods, corals and numerous gastropods imply marine conditions prevailed at times. The interbedding of these sediments points to a depositional system of shallow marine lagoons with numerous small islands or rapidly prograding supratidal areas in protected lagoons behind a reef-like barrier (Winter 1962, Hendricks and Wilson 1967:5, Stricklin et al. 1971, Young 1972:1).

The Glen Rose Limestone of Central Texas contains a scant ammonoid fauna which allows correlation with the European section (Young 1972:11, 1974:179). The Glen Rose Limestone is divided into upper and lower members by a bed (or zone of beds) containing numerous steinkerns of the bivalve *Corbula* (Stricklin et al. 1971:23).

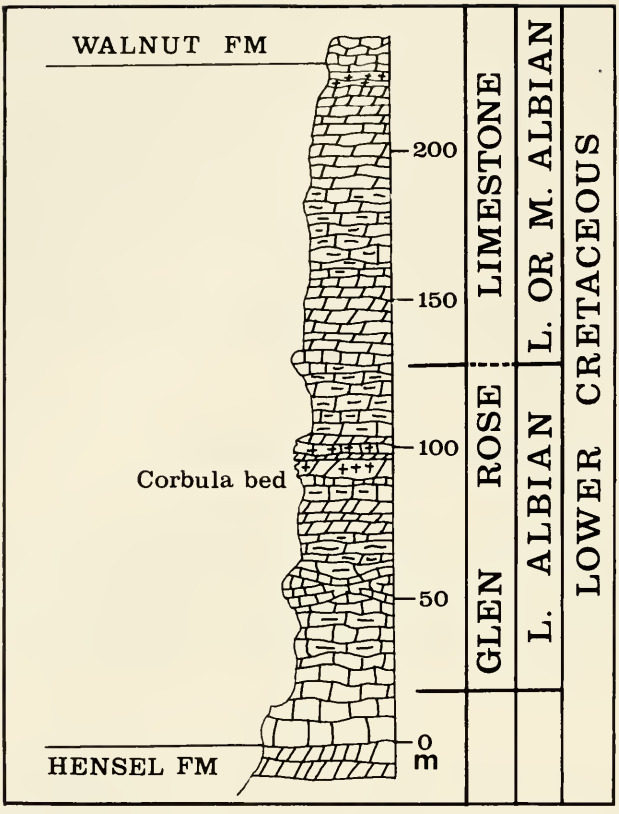

FIGURE 1. Lithostratigraphy and biostratigraphy of the Glen Rose Limestone (after Young 1974).

The "*Corbula*" bed is used in this study as a stratigraphic marker to locate the stratigraphic position of each collection. All of the Glen Rose Limestone below the *Corbula* bed and to a level of about 41 m (135 ft) above it are considered to be Early Albian by Young (1974:176). This includes all of the specimens described in this study.

LOCALITIES

Most specimens of decapods have been collected from 3 localities (Fig. 2). The specimens are from several collections: (GAB = Gale A. Bishop; SDSNH = San Diego Natural History Museum; WSA = W. S. Adkins; UT = University of Texas [Austin]).

The Nagle Locality (*GAB 21*).—This exposure was extensively collected by J. S. Nagle during the early 1960s. It is situated at the junction of Highways 290 and 281, about 9.7 km (6 mi) south of Johnson City, Blanco Co., Texas (Fig. 3).

Decapods occur throughout about 9 m (30 ft) of Glen Rose Limestone but are more abundant in an interval just below a *Corbula* bed and in a biomicrite about 7.6 m (25 ft) above the *Corbula* bed (Fig. 4).

Interesting assemblages of microscopic claws and dactyli were recovered from samples taken at points indicated in the measured section (Fig. 4). The microscopic decapod material is particularly abundant in the *Salenia texana* marl.

The associated fauna consists of numerous steinkerns of bivalves and gastropods.

Boerne-Sisterdale Locality (*GAB 25*).—This exposure is a road cut on Texas Farm Road 1376 at the top of a hill (Fig. 5) 12 km (7.5 mi) north of Boerne, Kendall Co., Texas. Approximately 9 m (30 ft) of Glen Rose Limestone is exposed in the road cut (Fig. 6). The road cut is about 37 m (120 ft) above exposures of the *Corbula* bed at the Hodges Range Section (GAB 26) 1.6 km (1 mi) to the northwest, and probably

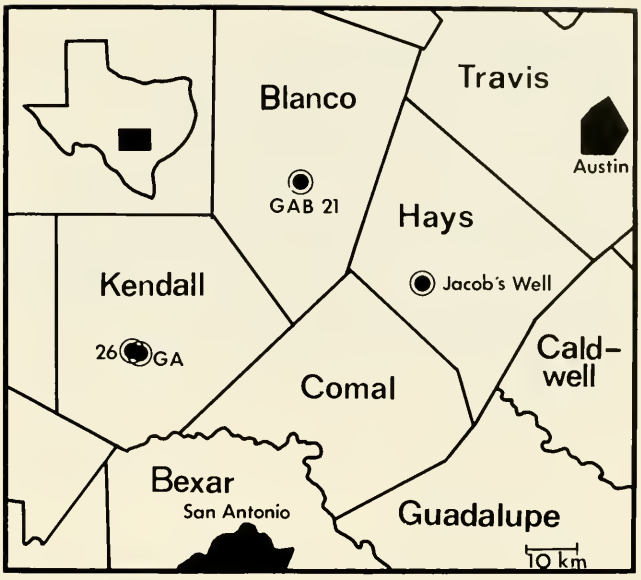

FIGURE 2. Index map of major collecting localities in Central Texas.

near the top of the fourth open shelf unit of Young (1974:177). Numerous remains of decapods were collected from a biomicrite near the bottom of the road cut (at arrow in Fig. 6).

Decapod remains occur throughout an interval 3 m (10 ft) in thickness but are most abundant in a 46 cm (18 in) bed of fossiliferous biomicrite. The specimens weather out of the platey marl and accumulate on the ledge formed by the underlying resistant bed.

The entire fauna has not been investigated in detail but numerous specimens of *Homomya* are present and preserved in living position. Other elements of the fauna include numerous pelecypods, gastropods, and masses of serpulid worm tubes.

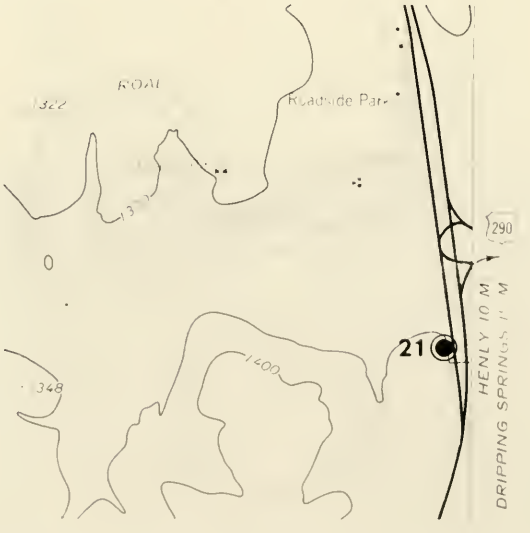

FIGURE 3. Topographic map of Nagle locality (GAB 21) 9.7 km (6 mi.) south of Johnson City at junction of U.S. Highways 290 and 281, Blanco Co., Texas. U.S.G.S. Monument Hill Quadrangle, scale 1:24 000, contour interval 20 ft (6.1 m).

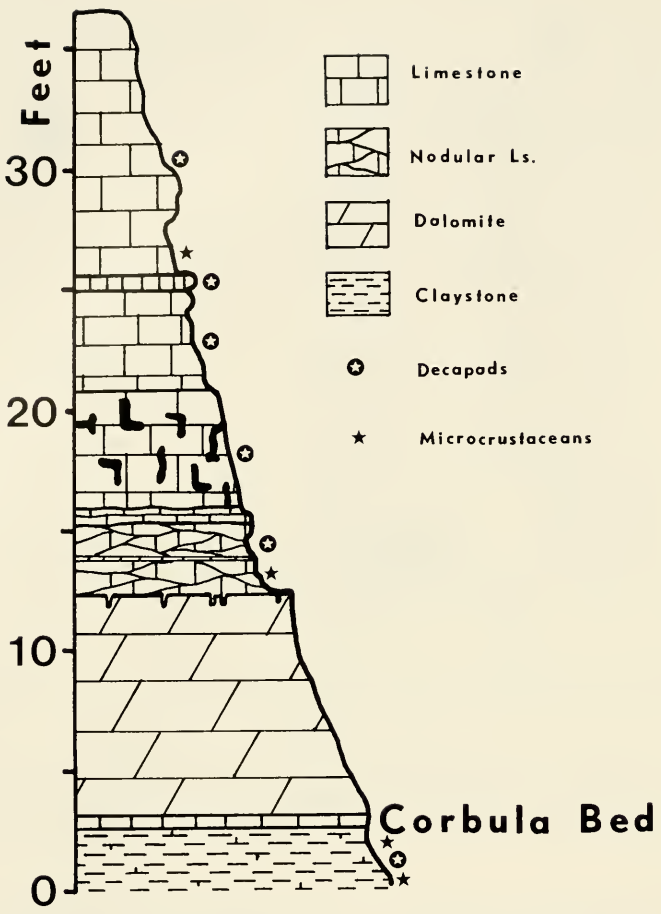

FIGURE 4. Measured section in Glen Rose Limestone at Nagle locality (GAB 21).

FIGURE 5. Topographic map of Boerne-Sisterdale (GAB 25) and Hodges Range (GAB 26) localities, 12.9 km (8 mi) north of Boerne on Farm Road 1376, Kendall Co., Texas. U.S.G.S. Sisterdale Quadrangle Scale 1:24 000, contour interval 20 ft (6.1 m).

FIGURE 6. Photograph of Boerne-Sisterdale outcrop (GAB 25), decapod interval marked by arrow. Vertical scale of foreground approximately 1 cm = 2 m (1″ = 17′).

The Hodges Range Locality (GAB 26).—The Hodges Ranch Locality (Fig. 5) is situated on the third tributary of Wasp Creek west of Texas Farm Road 1376 about 12.9 km (8 mi) north of Boerne, Kendall Co., Texas. Specimens were collected from a soft marl that contained *Salenia texana* just below a *Corbula* bed (Fig. 1). The locality also produced numerous sea urchins and some crinoids.

The outcrop is a semi-barren gentle slope (Fig. 7) just above a small creek. The surface is covered by great numbers of fossils, especially the heart urchin *Enallaster obliquatus*. Other faunal elements include oysters, gastropods, and bivalves.

The decapod part of the fauna from this locality is almost exclusively dominated by claws of the hermit crab, *Pagurus banderensis*. A collection of gastropod steinkerns was made to examine the possibility of preserved pagurids within the lithified mud of the steinkerns. No evidence of decapod exoskeleton was observed in the steinkerns. In fact, the steinkerns were packed with numerous shells and shell fragments mixed with carbonate mud. This suggests a fair amount of washing by currents or bioturbation after the shells were last occupied (by hermit crabs?) which would destroy evidence of any such occupation.

Other localities from which Glen Rose decapods have been collected are listed below:

1. Bandera-Pipe Creek Road (Texas Highway 16) 1.6 km (1 mi) east of Bandera, Bandera Co., Texas; *Salenia texana* zone. Rathbun 1935:39.

FIGURE 7. Photograph of Hodges Range locality (GAB 26). Collecting bag in center 38 cm (15 in.) high).

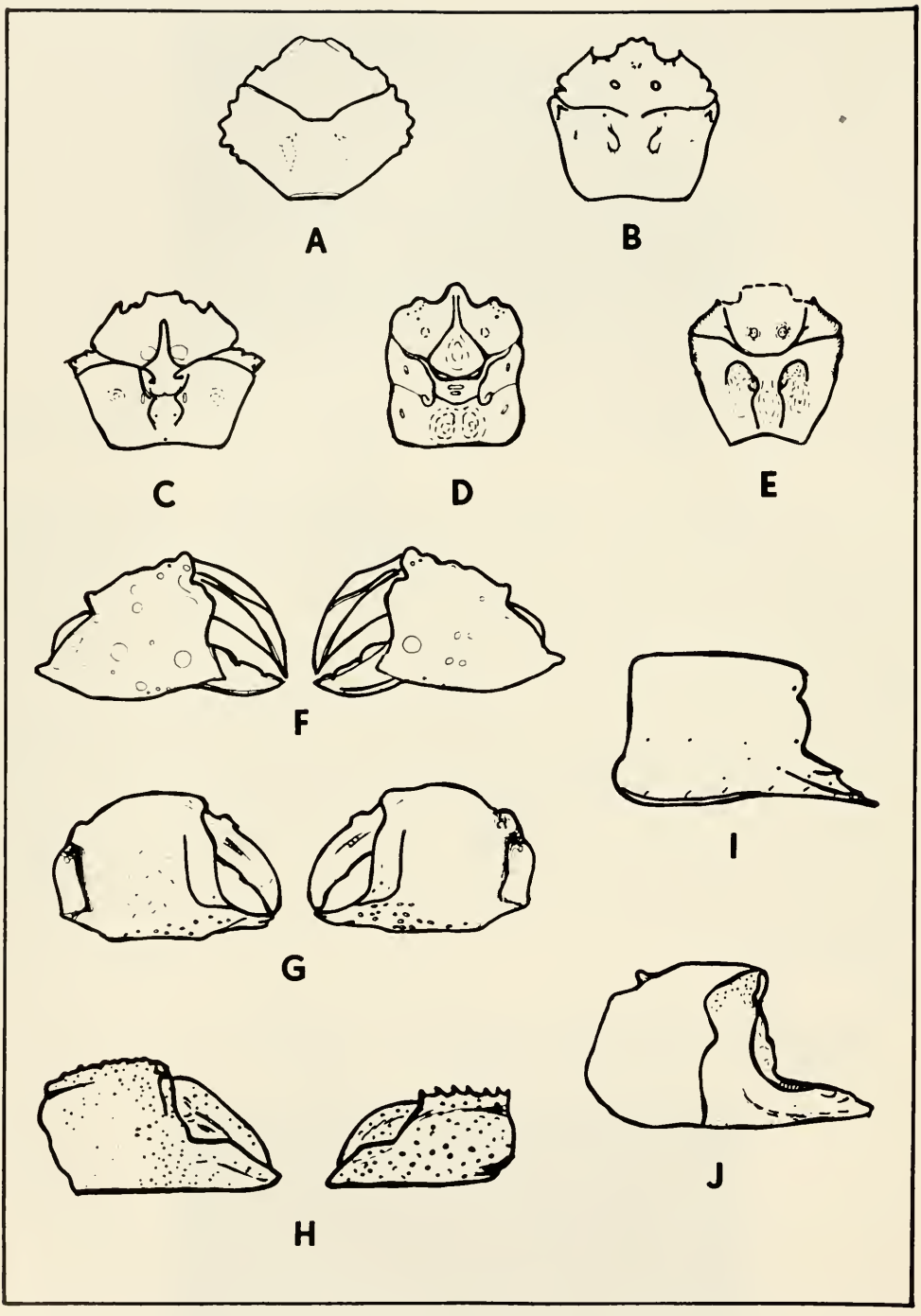

FIGURE 8. Line drawings of decapods from the Glen Rose Limestone, Central Texas. A, *Palaeodromites naglei* Bishop; B, *Pseudonecrocarcinus stenzeli* Bishop; C, *Hillius youngi* Bishop; D, *Dioratiopus scotti* Bishop; E, *Diaulax roddai* Bishop; F, *Prehepatus hodgesi* Bishop; G, *Roemerus robustus* Bishop; H, *Pagurus banderensis* Rathbun 1935; I, *Protocallianassa klofi* Bishop; J, *Torynomma? densus* Bishop.

2. Bandera-Pipe Creek Road (Texas Highway 16) 3.2 km (2 mi) east of Bandera; *Salenia texana* zone. Stenzel 1945:437.
3. "0.15 mile [0.24 km] south of state Highway No. 29 (Burnet-Austin road) and 0.07 mile [0.11 km] east of the Southern Pacific Railroad track 1.42 miles [2.27

TABLE 1. Tabulation of decapod collected from the Glen Rose Limestone.

	GAB–21	GAB–25	GAB–26	Other	Total
Protocallianassa sp.[a]	52	750	0	Yes[b]	802+
P. klofi	1	14	0	0	15
Pagurus banderensis[c]	1	12	10	7	30
Roemerus robustus	0	2	1	1	4
Palaeodromites naglei	1	8	0	0	9
Diaulax roddai	0	3	0	0	3
Hillius youngi	0	1	0	0	1
Dioratiopus scotti	0	0	0	1	1
Pseudonecrocarcinus stenzeli	0	6	0	0	6
Prehepatus hodgesi	1	27	2	0	30
Torynomma? densus	0	2	0	0	2

[a] Nearly whole palms.
[b] Numerous other localities yield *Protocallianassa*.
[c] Does not include movable fingers.

km] airline distance east of the courthouse in Burnet, Burnet Co., Texas." Stenzel 1945:437.

4. Junction of Highways 16 and 689, 2.6 km (1.6 mi) east of Bandera; *Salenia texana* zone; collected by Mrs. Henry W. Sebesta, sent to Keith Young by George His.
5. Blackman Ranch, Little Blanco River, Blanco Co., Texas; WSA 16215 collected by A. W. Cleaves.
6. Bluff of Blanco River, 4.8 km (3 mi) west of Blanco, Blanco Co., Texas; *Salenia texana* zone 1.5 m (5 ft) below *Corbula* Bed; UT 45488 (2 specimens) collected by N. B. Waechter.
7. Shingle Hills Section, Travis Co., Texas; *Salenia texana* zone; collected by G. L. Dawe.
8. From a limestone ledge about 1.5 m (5 ft) above water level at Jacob's Well, a spring on Cypress Creek, 1.5 km (3.2 mi) northwest of Wimberley, Hays Co., Texas, about 55 m (180 ft) below the Corbula Bed, Lower Glen Rose Limestone (calculated from Young 1974).

FAUNA

The decapod fauna (Fig. 8) of the Glen Rose Limestone consists of 11 taxa (Table 1). *Protocallianassa* sp. is the most abundant taxon, and *Pagurus* and *Prehepatus* are second most abundant. The decapod fauna at each locality forms only a part of a much larger fauna dominated by molluscs.

Preservation.—The fossil decapods of the Glen Rose Limestone are found as disarticulated fragments. Claws are most abundant but a few carapaces are present. The condition of the remains at the time of final entombment can not be determined. The presence of numerous decapod remains is probably due to the similarity of the mineralized exoskeleton and surrounding carbonate rocks. The mineralized exoskeleton is often only represented by a chalky carbonate material that weathers readily. This gives rise to many steinkerns (internal molds). Steinkerns of brachyurans reflect surface morphology but certainly differ significantly from specimens with exoskeletons. The finger tips of claws are often filled with sparry calcite signifying that they were not completely filled with mud at the time of burial.

Decapods.—The Glen Rose decapod fauna (Pls. 1–3) gives a crude measure of the diversity of decapods in North America in the Early Albian. Because of the small size of most of these decapods, they probably are seldom collected and, hence, the anticipated total decapod fauna certainly exceeds that described here. This fauna is the earliest Cretaceous decapod fauna described from North America.

The presence and abundance of hermit crabs (*Pagurus*) in these collections is due to their size, original abundance in the living fauna, and their heavy mineralization. The postulated shallow-lagoonal environment is very compatable with these shallow-water decapods. One specimen of *Pagurus* (Pl. 2, fig. 17) has an oyster attached to its claw. The lack of hermit crab fossils, except claws of pagurids, is due to the thin exoskeleton everywhere but on the heavily mineralized claws that function as an operculum to close the "borrowed" gastropod shells in which hermit crabs live. *Roemerus robustus* was also probably a hermit crab.

Because this is a large, new fauna there are several extensions of geographic range of the particularly well-known taxa from the Albian of England (Wright and Collins 1972). *Palaeodromites naglei, Diaulax roddai,* and *Pseudonecrocarcinus stenzeli* all extend the geographic ranges of the genera from Europe into North America. *Torynomma? densus* extends the range of that genus from Australia to North America. *Dioratiopus scotti* is the second described species of this taxon in North America (the other, *Dioratiopus dawsonensis* (Bishop 1973) is from the Maestrichian of Montana). A third species is present on the north flank of the Black Hills, low in the Pierre Shale.

Hillius youngi is so far known from 1 steinkern. It is hoped that additional material will substantiate the basic diagnostic features of this poorly represented taxon.

Prehepatus hodgesi joins other members of the genus, *P. cretaceous* and *P. pawpawensis* from the Early Cretaceous of Texas, and *P. dilksi* from the Late Cretaceous Merchantville Fm. of Maple Shade, New Jersey. The pattern and variability of ornamenting tubercles on these little claws is extremely interesting. Possibly the variation may be due to sexual dimorphism as in the fiddler crabs and perhaps may even have had some ritualistic or actual function in this crab's behavior.

Callianassids.—The most abundant decapod remains found in this collection and throughout the Glen Rose Limestone are thalassinids belonging to *Protocallianassa, Callianassa, Axius, Jaxea,* or some other closely related taxon. Only the chelae are represented in the collections from the Glen Rose Limestone.

The thalassinids are differentiated on the basis of carapace morphology, and chelation of walking legs. Within a given taxon (such as *Callianassa*) sexual dimorphism, differing morphology of right and left claws, intraspecific variation, and changes in morphology in different instars are all probable (Rathbun 1935:29). These factors seem to have combined to yield a baffling spectrum of chelae morphology. The claws found in the Glen Rose exhibit a wide variation. Morphotypes can be established easily but as the numerous specimens are examined the morphotypes become impossible to maintain. The claws will be analyzed again when a graphic analyzing computer system becomes available.

Microcrustaceans.—The presence of crustacean microfossils in the Glen Rose Limestone was pointed out to me by Peter Rodda while curating the collection of the Texas Bureau of Economic Geology. Subsequently, microfossil residues were prepared from the marls at each locality and numerous other Glen Rose localities. They demonstrated a diverse and abundant crustacean microfauna consisting of claws and dactyli (Pl. 3, fig. 44).

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PLATE I

FIGURES 1–2. *Diaulax roddai,* 1, Dorsal view of carapace, ×1.0; 2, Dorsal view stereo, ×2.0 SDSNH 23640 (orig. GAB 25, specimen 2). FIGURES 3–5. *Pseudonecrocarcinus stenzeli,* Dorsal view of latex cast of carapace; 3, ×1.0; 4, stereo, ×2.0; 5, view of impression of carapace in limestone, ×1.0, SDSNH 23641 (orig. GAB 25, specimen 8). FIGURES 6–7. *Dioratiopus scotti,* 6, Dorsal view of carapace, ×1.0; 7, Dorsal, stereo, ×2.0, SDSNH 23642 (orig. GAB 27, specimen 1). FIGURE 8–11. *Hillius youngi,* 8, Carapace, ×1.0; 9, Carapace, stereo, ×2.0; 10, Anterior of Carapace ×2.0; 11, Right side of carapace, ×2.0, SDSNH 23643 (orig. GAB 25, specimen 3). FIGURES 12–17. *Palaeodromites naglei,* 2–13, Carapace, Holotype SDSNH 23644 (orig. GAB 25, specimen 1); 12, ×1.0; 13, stereo, ×2.0; 14–17, Carapace features of specimen SDSNH 23645 (orig. GAB 21, specimen 21) collected by Nagle; 14, Dorsal, ×1.0; 15, Dorsal of carapace, ×2.0.

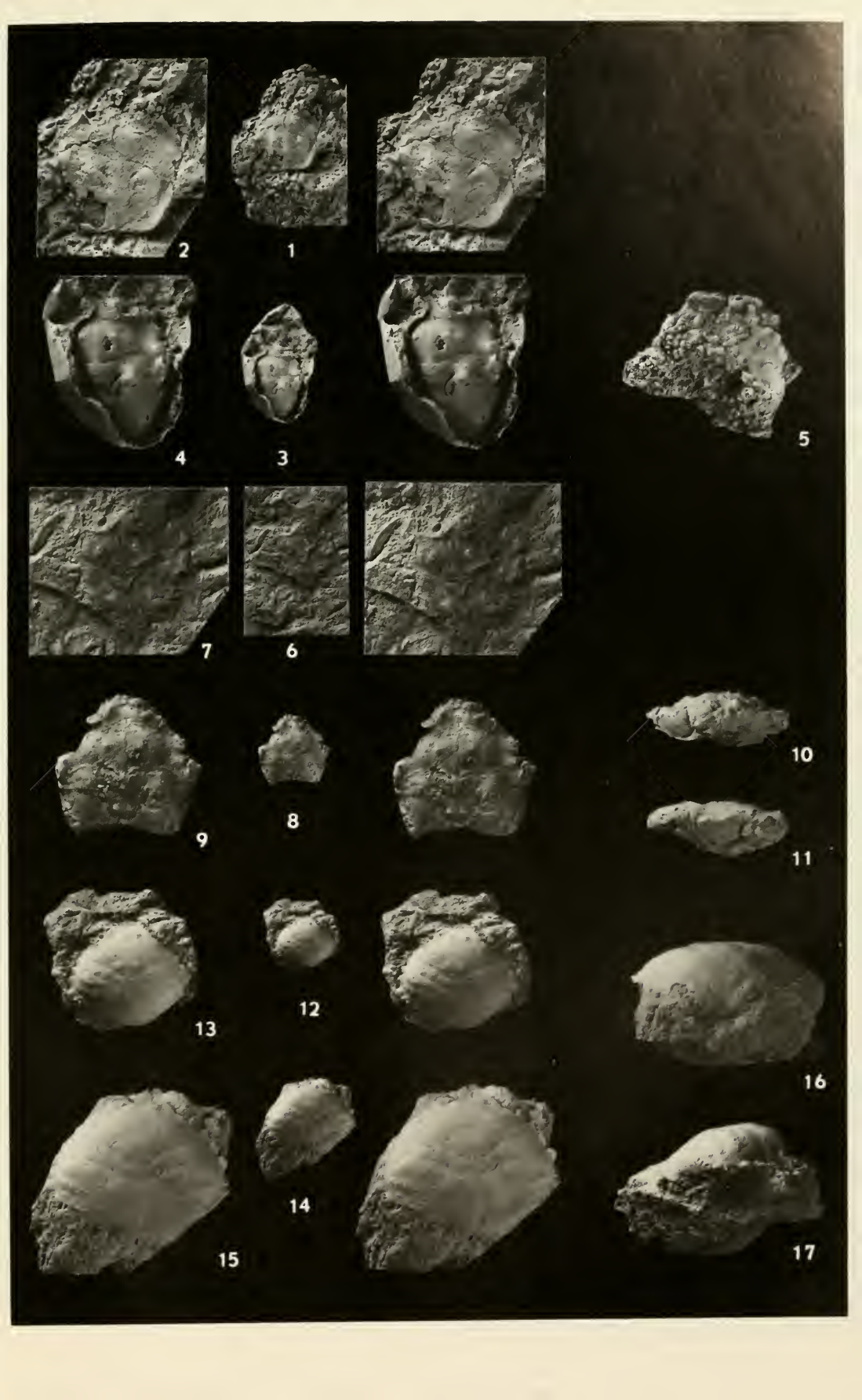
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TABLE 2. Measurements in millimeters of the major claw of *Protocallianassa klofi*.

Specimen*	Right or left	Propodal length (mm)	Palm length (mm)	Palm height (mm)
25–67	R	13.7	9.8	7.7
25–160	R		8.0	7.0
25–153	L		9.2	8.6
SDNHM 23665 (=25–152)	R		9.2	8.5
25–87	L		10.7	9.8
25–116	R	15.6	11.0	9.2
25–133	L		10.8	9.3
25–124	L	10.9	7.0	6.0
25–123	R	9.8		6.6
25–144	R			
25–127	R		8.2	5.8
25–164	R	8.1	6.8	5.4
25–136	L	8.5	6.7	5.8

* Specimens in the tables are listed by locality number followed by the specimen number (e.g. 25–67 is locality GAB25, specimen 67).

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille 1803
Suborder Pleocyemata Burkenroad 1963
Infraorder Anomura H. Milne-Edwards 1832
Superfamily Thalassinoidea Latreille 1831
Family Callianassidae Dana 1852
Subfamily Protocallianassinae Beurlen 1930
Genus *Protocallianassa* Beurlen 1930

Type species.—*Callianassa archiaci* A. Milne-Edwards 1860 by original designation.

Diagnosis.—"Carapace with *linea thalassinica*; first pereiopods with well developed chelae, hetereochelous; abdomen with pleura developed on second to sixth somites; uropods without diaeresis . . . (Single chelae are hardly distinguishable from those of *Protaxius* or *Callianassa*)." (Glaessner 1969:478).

Protocallianassa klofi new species
Pl. 3, figs. 41–43; Fig. 8I; Tab 2

Type.—The holotype, a right major propodus (orig. GAB 25, specimen 152) is deposited in the San Diego Natural History Museum (SDNHM 23665).

→

PLATE 2

FIGURES 1–16. Right chelae of Pagurus banderensis. 1–5, Specimen SDSNH 23646 (orig. GAB 25, specimen 7). 1, Outer face; 2, Inner face, 3, Bottom, and 4, Top; ×2.0. 5, Outer face, ×1.0. 6–8, Specimen SDSNH 23647 (orig. GAB 21, specimen 17). 6, Outer face and 7, Inner face; ×2.0; 8, Outer face, ×1.0. 9–12, Specimen UT 45473 (Univ. Texas, Austin). 9, Outer; 10, Inner; 11, Lower; and 12 Top, ×1.0. 13–15, Specimen SDSNH 23648 (orig, GAB 26, specimen 5). 13, Outer; 14, Inner; and 15, Top ×2.0. 16, Specimen WSA 16215 (Univ. Texas, Austin), Outer face with walking leg, ×1.0. FIGURES 17–25. Left chelae of *Pagurus banderensis*. 17, Specimen SDSNH 23649 (orig. GAB 26, specimen 3), Inner face of left claw with attached oyster, ×2.0. 18, Specimen SHSNH 23650 (orig. GAB 26, specimen 4). Outer face of propodus, ×1.0. 19, Specimen UT 45488, Outer face of claw, ×1.0. 20–21, Specimen SDSNH 23651 (orig. GAB 25, specimen 11), Outer (20), Inner (21), faces of nearly complete minor claw, ×1.0. 22–25, Specimen SDSNH 23652 (orig. GAB 26, specimen 1), Outer (22), Inner (23), Bottom (24), and Top (25) views, ×2.0. FIGURES 26–31. Dactyli of *Pagurus banderensis*. 26–29, Specimen SDSNH 23653 (orig. GAB 26, specimen 12), Dactylus of walking leg, ×2.0. 30–31, Specimen SDSNH 23654 (orig. GAB 26, specimen 11), Dactylus of major claw, 30, Side ×1.0 and 31, Occlusional surface, ×2.0.

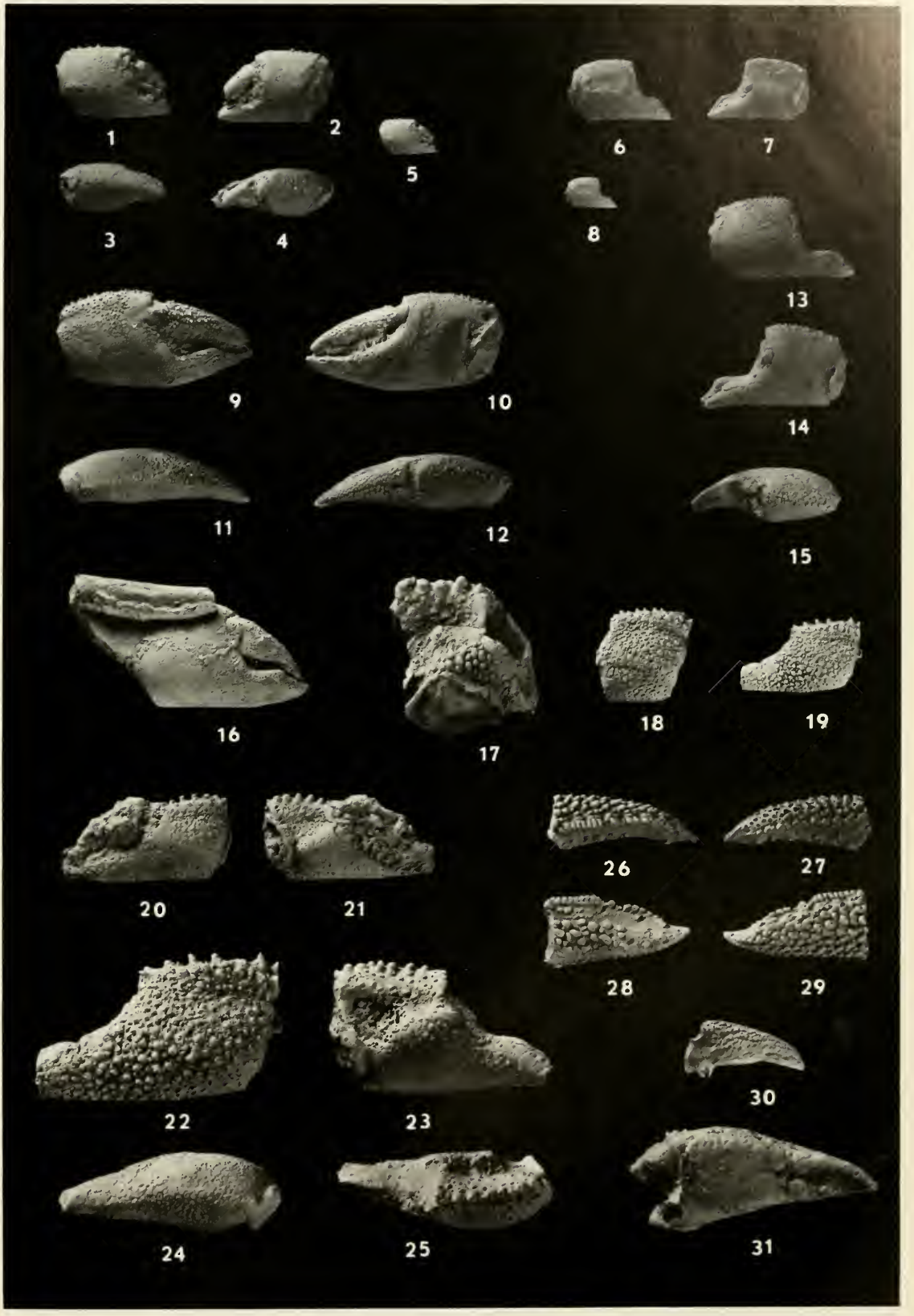
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TABLE 3. Height (H), length (L), thickness (T) in millimeters, and height/thickness (H/T) ratios of claws of *Pagurus banderensis*.

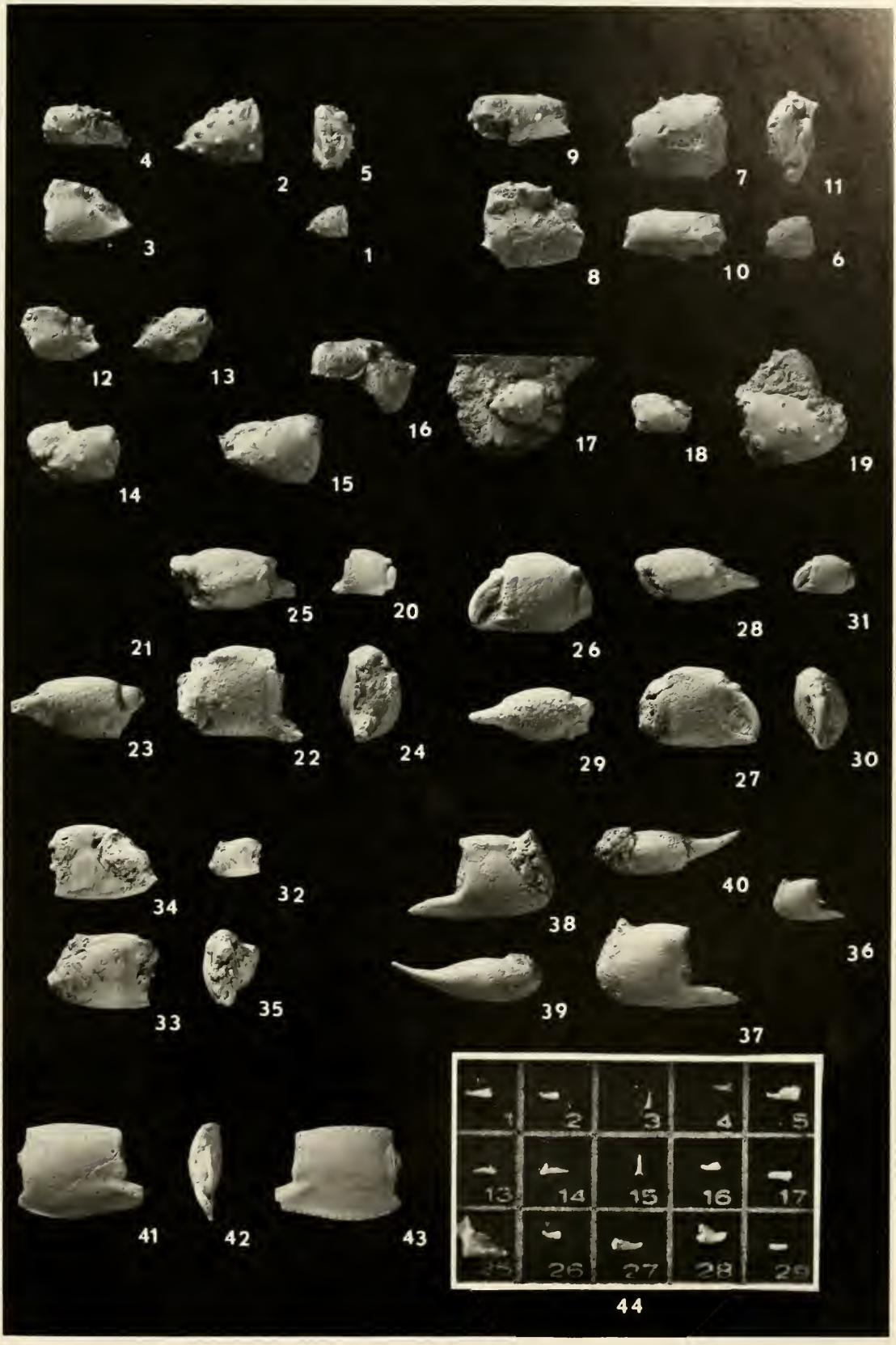
	Height (mm)	Length (mm)	Thickness (mm)	H/T*
Right Claw				
25–22	3.7	5.5	1.9	1.90
25–23	4.2	7.3	2.5	1.70
SDNHM 23647 (=21–17)	4.9	8.6	2.3	2.09
25–25	5.4	9.8	3.6	1.52
25–24	5.6	7.5*	3.4	1.65
SDNHM 23646 (=25–7)	6.0	9.74+	4.0	1.51
25–26	10.2	15.7*	6.3	1.62
25–28	10.6	19.2		
26–14	10.8		7.2	1.49
25–27	11.9	18.7	5.7	2.09
SDNHM 23648 (=26–5)	13.8	23.8	9.0	1.54
Stenzel	14.2	26.7	9.0	1.57
UT 45473	16.3	32.4	9.3	1.75
26–16	17.0		11.1	1.53
WSA 16215	17.9	30.2*	11.4	1.57
26–6	19.7		11.8	1.67
26–19	20.0		11.8	1.69
Stenzel**	22.8		10.8	2.11
Left Claw				
SDNHM 23651 (=25–11)	7.1	14.3	4.47	1.56
Stenzel	7.4	16.2	5.1	1.45
25–31	7.5	10.8*	4.94	1.51
25–30	7.5*		5.12	1.46
25–29	7.6	15.2*		
26–15	10.1		6.27	1.61
26–7	10.3	16.8+	7.34	1.40
SDNHM 23652 (=26–1)	10.9	17.9	6.50	1.67
SDNHM 23649 (=26–3)	11.4		7.8	1.46
26–2	11.5		7.4	1.55
UT 45488	11.8	20.5*	8.86	1.33
UT 45488	13.9	19.8*	8.90	1.56

* Calculated before rounding thickness measurements from hundreths of a mm.
** Stenzel's holotype of *P. travisensis*.

→

PLATE 3

FIGURES 1–19. *Prehepatus hodgesi*. 1–5, Holotype, Specimen SDSNH 23655 (orig. GAB 25, specimen 14); Outer surface of propodus, ×1.0, 2–5, Outer, Inner, Top, and Distal views of propodus, ×2.0. 6–11, Specimen SDSNH 23656 (orig. GAB 26, specimen 9); 6, Outer face of propodus, ×1.0; 7–11, Outer, Inner, Top, Bottom, and Distal views, ×2.0. 12–13, Specimen SDSNH 23657 (orig. GAB 25, specimen 16); 12, Inner face and 13, Outer face of propodus, ×2.0. 14–16, Specimen SDSNH 23658 (orig. GAB 25, specimen 137), articulated carpus and propodus in oblique (14), Front, (15), and Top view (16), ×2.0. 17, Specimen SDSNH 23659 (orig. GAB 21, specimen 22), complete propodus and disarticulated dactylus in front view, ×2.0. 18, Specimen SDSNH 23660 (orig. GAB 25, specimen 18), left propodus in front view, ×2.0. 19, Specimen SDSNH 23661 (orig. GAB 25, specimen 15), left propodus in front view, ×2.0. FIGURES 20–31. *Roemerus robustus*. 20–25, Specimen SDSNH 23662 (orig. GAB 26, specimen 8). 20, Outer view, ×1.0. 21–25, Views of outer face, inner face, bottom, distal end, and top of left propodus. 26–31, Holotype, Specimen UT 45704. 31, Outer view, ×1.0. 26–30, Outer, inner, top and bottom views, ×2.0. FIGURES 32–40. *Torynomma? densus*. 32–35, Paratype Specimen SDSNH 23663 (orig, GAB 25, specimen 10), 32, Outer view, ×1.0. 33–35, Outer, inner and distal views ×2.0. 36–40, Holotype, right propodus, Specimen SDSNH 23664 (orig. GAB 25, specimen 5), 36, outer, ×1.0. 37–40, Outer, inner, bottom, and top views, ×2.0. FIGURES 41–43. *Protocallianassa klofi*. Holotype, Right major propodus, Specimen SDSNH 23665 (orig. GAB 25, specimen 152). 41–43, Outer, distal, and inner views, ×2.0. FIGURE 44. Slide of microcrustacean appendage elements, ×3.25.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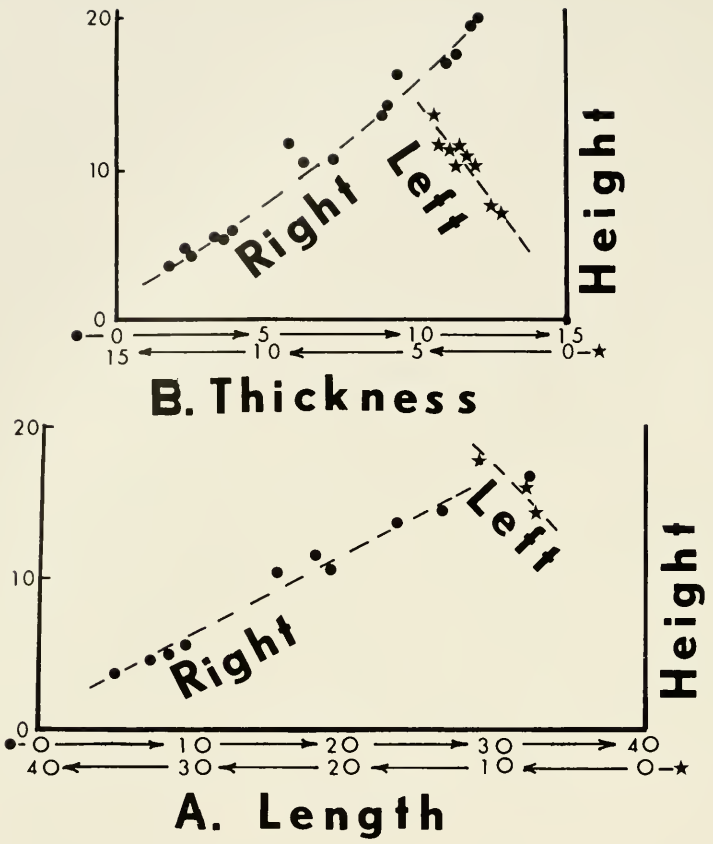

FIGURE 9. Graph of A. height (mm) vs. length (mm) (bottom) and B. height (mm), vs. thickness (mm) of *Pagurus banderensis* Rathbun 1935. Right claws plotted as dots (read thickness or length on upper scale increasing from left to right) and left claws as stars (read thickness of length on lower scale increasing from right to left).

Occurrence, sample size, and preservation.—Fourteen specimens of this taxon were collected at GAB 25 and 1 at GAB 21. Most are preserved as single isolated propodi with chalky exoskeleton over a firm micrite filling.

Etymology.—Named in honor of L. R. Klof, Texas sedimentologist, who often exhibited nocturnal and fossorial habits.

Description.—Propodus flat, broad, nearly twice as long as high. Palm rectangular, slightly longer than high, thin. Upper margin bowed slightly into convex arch. Proximal (carpal) edge nearly vertical. Distal margin slants slightly outward to top of short fixed finger. Two sinuses present on back of hand along margin; uppermost about ½ the distance to top of the fixed finger, the second lies immediately above fixed finger. Lower margin convex proximally and concave beneath base of fixed finger. Lower proximal corner produced into a rounded projection. Propodus convex on outer face (back of hand), nearly flat on inner face (palm). Convexity of outer face continues onto rounded upper margin which overhangs inner side (palm) forming a shallow depression along top of inner side (palm) parallel to upper margin. Another shallow depression parallels the wedge-shaped lower margin on palm. Lower margin of outer side produced into a narrow keel from proximal edge almost to base of fixed finger.

Fixed finger short, nearly horizontal and turned inward. Most large specimens with auxillary ridge along outer edge of occlusional surface of fixed finger, terminating in tooth-like projection. An oblique ridge runs off propodus onto fixed finger on back of hand (outer side and on palm [inner side]).

Convex outer face ornamented by 4 or 6 large hair pits along ridge running onto finger. Four hair pits arranged in a horizontal row just above level of sinus immediately above base of fixed finger. One hair pit situated just above uppermost sinus. Three hair pits form broad-based isosceles triangle just below proximal edge of finger ridge. Four to 8 hair slits slant upward and distally along lower margin just above fine keel.

Palm (inner face) has approximately 10 downward and distally slanting hair slits along upper margin just beneath overturned angulated edge where flat palm meets the convex outer face. Approximately 15 hair slits slanting upward and distally situated along lower edge of palm.

Comparison.—*Protocallianassa klofi* is similar to *P. praecepta* Roberts 1962 but differs from it by having a relatively shorter palm, a rounded lower proximal corner, and lacking the ridge at the base of the fixed finger on the inner face.

Remarks.—The minor chela of this taxon is not as yet known. No pairs of chelae were found preserved together to directly tie the major and minor chelae to one another.

Protocallianassa sp.

The majority of the specimens referrable to *Protocallianassa* comprise a highly variable series of chelae. Attempts to differentiate morphotypes failed except in the case of *P. klofi* because gradations were found between all other morphotypes I attempted to establish.

The claws vary from proximally expanded, through rectangular, to nearly oval in shape. The cross-sectional shape varies from biconvex, through convex on the other face, to spatulate. The fixed fingers are usually curved slightly inward. Ornamentation by hair pits is extremely variable.

Superfamily Paguroidea Latreille 1803
Family Paguridae Latreille 1802
Subfamily Pagurinae Latreille 1802
Genus Pagurus Fabricius 1775

Type species.—"*Cancer bernhardus* Linne 1758" (on official list, ICZN); subsequent designation Latreille 1810 =*Eupagurus* Brandt 1851 (type, *Cancer bernhardus* Linne' 1758; subsequent designation Stimpson 1858) (obj.)." (Glaessner 1969:R479).

Diagnosis.—"Chelipeds usually dissimilar and unequal, right being much larger than left, very rarely subequal; 4th periopods subchelate." (Glaessner 1969:R479).

Pagurus banderensis Rathbun 1935
Pl. 2, figs. 1–31; Figs. 8H, 9; Tab. 3

Pagurus banderensis Rathbun 1935, p. 39, Pl. 9, figs. 7, 8.
Pagurus banderensis (Rathbun); Stenzel 1945, p. 435, Pl. 45, figs. 7–15.
Palaeopagurus banderensis (Rathbun); Roberts 1962, p. 175.

Occurrence.—Specimens of *Pagurus banderensis* have been collected at many localities including GAB 21, GAB 25, GAB 26, and Localities 1–7.

Previous descriptions.—*See* Rathbun 1935:30 and Stenzel 1945:435–437.

Remarks.—The collections made at GAB 25 and GAB 26 give the first suites of specimens of *P. banderensis*. Height, length, and thickness data were gathered (Table 3) and are presented graphically in Fig. 9.

Size variation is much greater in the right claw than in the left claw. This generalization also carries over to their morphology and ornamentation; the right claws are highly variable in shape, cross section, and degree of granulation, whereas the left claws are more consistent in shape and ornamentation. Small right (major) chelae tend to have a straighter lower margin which becomes gently convex as size increases. There seems to be a tendency for a single row of upper margin granules in small sizes and 2 distant rows (surrounded by many smaller granules) in larger specimens.

Two specimens (GAB 21, specimen 17 and GAB 25, specimen 27) are thinner

TABLE 4. Measurements in millimeters of claws of *Roemerus robustus*.

	Total length (mm)	Height (mm)	Palm length (mm)	Thickness (mm)	Claw
UT 45704	10.5	7.75	6.75	4.5	Left
SDNHM 23662 (=26–8)	10.4	8.9	7.8	5.1	Left
25–162	6.7	5.0	4.7	2.6	Right
25–163	6.8	5.1	4.6	3.2	Left
25–165	6.3	5.8	8.3	3.9	Right

than the others (H/T-1.62) and might have been called *P. travisensis* (H/T-2.11) by Rathbun. I consider these thinner specimens to be *P. banderensis* until such time as sufficient material becomes available to clearly separate them as *P. travisensis* upon the basis of shape, or until the left (minor) claw of *P. travisensis* can be demonstrated to exist.

One other specimen (GAB 25, specimen 26) is different enough to merit special consideration. The upper margin is narrow and the claw pear-shaped in cross section. In front view the lower margin is straight and the upper and lower margins highly divergent.

A walking leg is preserved with a large major chela (Pl. 2, fig. 16). A fragment of a dactylus of a walking leg is also figured (Pl. 2, figs. 26–29). A fairly common element in the collections is the movable finger belonging to this taxon (Pl. 2, figs. 30–31).

Family Paguridae Latreille 1802
Subfamily Uncertain
Roemerus new genus

Type species.—*Roemerus robustus* new species.

Diagnosis.—Chelae elongate, similar, with rectangular palm, outer face transversely convex, inner flat. Carpal and dactyl articulations perpendicular to lower margin which is straight except for convexity below base of fixed finger. Fingers short and turned slightly inward. Fixed finger has at least 1 proximal tooth. Tip of movable finger overlaps fixed finger in smaller claws and closes onto outer edge of tip in large claws. Surface sparsely covered with large, low granules which become numerous and prominent on lower edge. The upper surface surmounted by a low, oblique ridge accentuated on the proximal inner face by a few low granules and becoming less conspicuous as it runs toward the top center of the distal margin of the claw.

Etymology.—In honor of Ferdinand Roemer, pioneer geologist and paleontologist of Texas and México.

Comparison.—This claw is similar to *Palaeopagurus* Van Straelen 1925 but differs in being more rectangular, having a more vertical distal margin, and having a slightly upturned fixed finger instead of slightly downturned. *Roemerus robustus* is easily distinguished from *Pagurus banderensis* Rathbun 1935 by its rectangular shape.

Roemerus robustus new species
Pl. 3, figs. 20–31; Fig. 8G; Tab. 4

Types.—The holotype, a left propodus and dactylus (UT 45704), was collected by G. L. Dawe from the *Salenia texana* marl at Shingle Hills, Travis Co., Texas. The paratype, a left propodus (orig. GAB 26, specimen 8), was collected at GAB 26. The holotype is deposited at the Univ. of Texas (Austin) as UT 45704. The paratype is deposited in the San Diego Natural History Museum (SDSNH 23662).

Occurrence, sample size, and preservation.—Five specimens of *Roemerus robustus* were available for description; 1 from Shingle Hills (UT 45704), 1 from (GAB 26), and 3 from (GAB 25).

Etymology.—The name is taken from the robust nature of the claws of this taxon.

Description.—Claws robust, similar, rectangular, and thick. Palm slightly longer

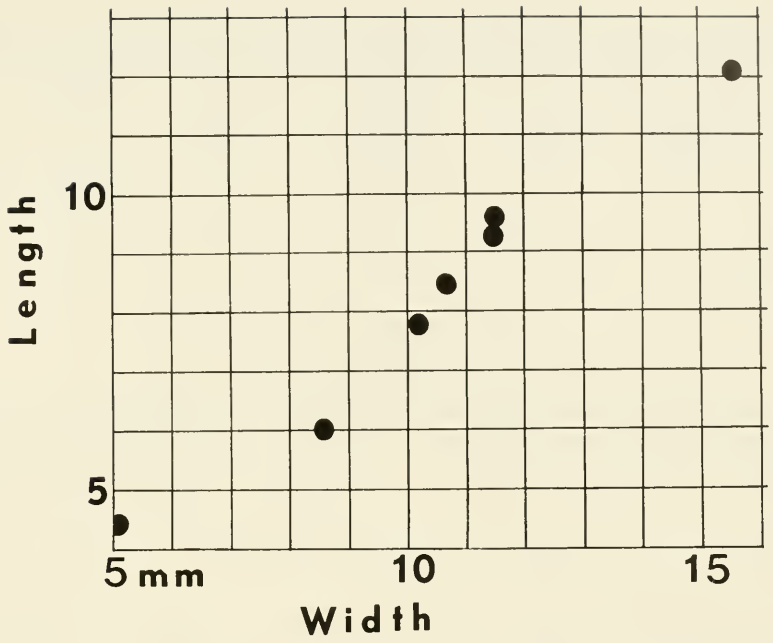

FIGURE 10. Graph of carapace width (mm) vs. length (mm) of *Palaeodromites hodgesi* Bishop.

than high and fingers short, slightly incurved, movable finger overlapping tip of fixed finger.

Lower edge straight except for slight convexity below base of fixed finger. Proximal edge perpendicular to lower margin. Distal edge, above the fixed finger vertical. Upper margin convex, especially proximally, where it curves down onto prominent carpal articulator.

Outer face transversely convex and ornamented by broad ridges along proximal and distal edges formed by narrow furrows on inside. Surface covered by sparse, large, subdued granules except for lower edge which has numerous, large, prominent granules.

Inner face relatively flat and ornamented by a distal ridge and a bend in the exoskeleton near proximal margin forming a groove.

Upper margin surmounted by an oblique ridge which runs from outer-distal corner to inner-proximal corner and is progressively more pronounced proximally until it forms a noticeable low ridge on upper edge of inner face. A few large granules may accentuate ridge.

At least 1 tooth can be seen situated on fixed finger near its base.

Comparison.—*Roemerus robustus* differs from most other pagurids by having a pronounced rectangular shape. Only *Palaeopagurus* Van Straelen 1925 and *Petrochirus* Stimpson 1859 even approach this shape.

Infraorder Brachyura Latreille 1803
Section Dromiacea deHaan 1833
Superfamily Domiodea deHaan 1833
Family Dynomenidae Ortmann 1892
Genus *Palaeodromites* A. Milne-Edwards 1865

Type species.—By monotypy; *Palaeodromites octodentatus* A. Milne-Edwards 1865, p. 345, pl. 5; Hauterivian of France.

Diagnosis.—Carapace broader than long, rounded pentagonal or hexagonal, widest two-thirds from front, gently arched transversely and longitudinally. Front square to trapezoidal, turned strongly downward; orbits large, oval, widely spaced. Anterolateral

TABLE 5. Measurements in millimeters of the carapace of *Palaeodromites naglei*.

Specimen	Length (mm)	Width (mm)
SDNHM 23644 (=25–1)	8.5	10.7
25–4	9.3+	11.5+
25–52	6.0?	8.6?
25–53	7.8+	10.2
25–54	4.4	5.1
25–57	9.6+	11.5
SDNHM 23645 (=21–21)	12.1	15.6

borders convex with tooth-like spines or lobes, posterolateral borders short, straight, or concave without tooth-like lobes, hind margin short, straight, or concave. Cervical furrow clearly defined, sinuous to straight; branchiocardiac furrows weakly defined. (After Wright and Collins 1972:49).

Palaeodromites naglei new species
Pl. 1, figs. 12–17; Figs. 8A, 10; Tab. 5

Types.—The holotype SDSNH 23644 (orig. GAB 25, specimen 1) and paratype SDSNH 23645 (originally GAB 21, specimen 21) of *Palaeodromites naglei* are both carapaces and are deposited in the San Diego Natural History Museum.

Occurrence, sample size, and preservation.—*Palaeodromites naglei* has been found at GAB 21 and GAB 25.

Etymology.—In honor of J. Stuart Nagle, who discovered the first specimen of this taxon.

Description.—Carapace hexagonal, 1.2 times wide as long, very convex longitudinally, less convex transversely. Carapace furrows poorly developed, a faint cervical furrow and 3 branchial furrows present. Rostrum rounded, nearly vertical. Orbits poorly defined in dorsal view arching upward. Width between outer angles of orbits 57% carapace width. Mesogastric region barely set off from rest of cephalic arch. Three faint grooves on branchial region parallel cervical furrow. Metagastric and protogastric regions set off from the cardiac and branchial regions by faint muscle attachment scars. Hind margin paralleled by a marginal groove.

Branchial regions split into 4 fields by very faint grooves; anteriormost parallels the cervical furrow to a point behind outer angle of orbit then banks backward and outward to back of first lateral spine. Second groove beginning at anterior end of muscle attachment field, trends outward to first lateral spine. Third furrow extremely faint, lying just inside a ridge paralleling posterolateral margin.

Anterolateral margins each composed of 4 forward facing broad spines which get progressively larger posteriorly; the first little more than a broadening of the carapace edge just behind outer angle of orbit, the second asymmetrical, bent sightly forward, the third the shape of an equilateral triangle, and the fourth broadly rounded, forming the widest part of carapace.

Posterolateral margin serrated by a series of 3 or 4 spines which decrease rapidly in size to the last which is little more than a granule, anteriormost a small spine on the dorsal shield edge about the size of second anterolateral spine.

The ventral side and appendages presently unknown because none of these parts definitely attached to a carapace.

Comparison.—*Palaeodromites naglei* is much smoother and less ornamented than other species of this genus. *Palaeodromites naglei* is additionally distinguished from *P. sinusosulcatus* Wright and Collins 1972 by a straight cervical furrow and lower convexity, from *P. incertus* (Bell 1863) by the lack of coarse granulation, and from *P. transiens* Wright and Collins 1972 by the lack of posterolateral ornamentation.

TABLE 6. Carapace measurements in millimeters of *Diaulax roddai*.

Specimen	Width (mm)	Length from front orbit to hind margin (mm)	Orbital width (mm)	Rostral	
				Width (mm)	Length (mm)
SDNHM 23640 (= 25–2)	10.6	10.7	6.8		
25–58	5.8		4.0	1.6	1.0+
25–161	6.6	6.1+	4.2		

Family Diaulacidae Wright and Collins 1972
Genus *Diaulax* Bell 1863

Type species.—*Diaulax carteriana* Bell 1863, by original designation.

Diagnosis.—"The carapace is more or less hexagonal, widest just in front of or just behind the ends of the cervical furrow, in longitudinal section curved more or less steeply down anteriorly but flat posteriorly, in transverse section flat. The front is generally downturned, pointed or squared; it may be sulcate with the edges turned up into prominent lobes or nearly flat. The antero- and posterolateral margins are very sharp, not lobed and with only a few small, sharp spines directed forwards. The cervical and branchiocardiac furrows are weak and tend to be straight and transverse. The regions are poorly defined. The surface is very finely granulate." (Wright and Collins 1972:56).

Diaulax roddai new species
Pl. 1, figs. 1–2; Fig. 8E; Tab. 6

Type.—The holotype, a partial carapace (orig. GAB 25, specimen 2) is deposited in the San Diego Natural History Museum, SDSNH 23640.

Occurrence, sample size, and preservation.—The holotype is 1 of 3 specimens of this taxon thus far collected. It is an almost complete carapace missing only the rostrum and left rear corner of the carapace. The exoskeleton is preserved as a chalky limestone and does not show surface ornamentation very well. One specimen (GAB 25, specimen 58) has a partly preserved rostrum and the third specimen (GAB 25, specimen 161) is a poorly preserved, crushed carapace.

Etymology.—For Peter U. Rodda, Curator of Geology, California Academy of Sciences, whose encouragement led to the completion of this study.

Description.—Carapace kite-shaped with truncated anterior and posterior slightly longer than wide, widest about ⅓ distance from front. Large specimens flat with raised anterolateral margins turned slightly under the dorsal shield on pterygostomial regions; smaller specimens with higher relief.

Cervical groove indistinct except for notch where it meets edge of the dorsal shield near widest part of carapace. Epimeral muscle scars present but not deeply incised.

Regions poorly differentiated; rostrum fairly broad, long. Cephalic arch dominated by spines at outer edges of orbits and raised anterolateral margins running from orbital spines to cervical notch. Gastric areas slightly higher than rest of cephalic arch with slight protogastric bosses. Distance between outer edges of orbits ⅔ the carapace width. Scapular arch flat, undifferentiated except for epimeral muscle scars and slight bosses distal to epimeral peninsulas, forming ridges that continue almost to hind margin.

Anterolateral margins dominated by large upward and forward pointing spines at outer edge of upward turned orbits that have a single fissure on lower edge, raised margin concave to cervical notch. A large upward, forward pointing spine and a second, smaller spine lie on margin behind cervical notch (second spine about same distance behind notch as orbital spine is ahead of it). Dorsal shield margin convex to first scapular spine and runs almost in a straight line to concave V-shaped posterior margin. Hind margin bordered by furrow.

Comparison.—*Diaulax roddai* is distinguished from *D. oweni* (Bell 1850) and *D. carteriana* Bell 1863 by being relatively longer and more flat, especially longitudinally. *Diaulax roddai* most resembles *D. feliceps* Wright and Collins 1972 but is relatively longer, has its maximum width further forward, and has a longer rostrum.

Remarks.—Small specimens of this taxon appear to have a better differentiated carapace than larger specimens.

Superfamily Dorippoidea de Haan 1841
Family Dorippidae de Haan 1841
Subfamily Dorippinae de Haan 1841
Hillius new genus

Type species.—*Hillius youngi* new species

Diagnosis.—Carapace pentagonal, fairly flat, slightly wider than long, widest half the distance from front. Grooves broad and indistinct. Rostrum broad. Orbital width 50% carapace width, orbits small, upturned, notched near inner corner, with raised rim. Epibranchial areas wide, giving specimens a wing-like or ray-like appearance.

Etymology.—For Robert Thomas Hill, pioneer Texas geologist, stratigrapher, and paleontologist.

Comparison.—This taxon has a striking resemblance in carapace shape to *Dorippe* Weber 1795, *Goniochele* Bell 1858, and *Orthopsis* Carter 1872. It differs from *Dorippe* by having a wider front with convex anterolateral margins. *Hillius* differs from *Goniochele* by having the widest part of the carapace relatively more forward and formed by the epibranchial lobes. *Hillius* is most similar to *Orthopsis* but differs from it by its having less relief, lack of anterolateral spination, and single orbital lobe.

Hillius youngi new species
Pl. 1, figs. 8–11; Fig. 8C

Type.—The Holotype, a carapace steinkern (orig. GAB 25, specimen 3), is deposited in the San Diego Natural History Museum (SDSNH 23643).

Occurrence, sample size, and preservation.—The Holotype is the only specimen of this taxon's carapace that is nearly complete. The specimen was collected at GAB 25. As with any description from decortiated specimens only major ornamentation features are likely to be decipherable, and a specimen with exoskeleton will be needed to completely define this taxon.

Etymology.—In honor of Keith Young, Texas Cretaceous stratigrapher and paleontologist.

Description.—Carapace pentagonal, probably slightly wider than long (partial length 11.5 mm), widest about half the distance from the front. Carapace slightly convex longitudinally; cephalic arch moderately convex transversely, scapular arch fairly flat transversely, except at the edges.

Cervical furrow broad and indistinct except where it crosses dorsal shield margin in a pronounced notch continuing on subhepatic region as a well-defined groove to base of orbit. An indistinct groove on subhepatic region lies above and is parallel to cervical furrow. Faint but distinct mesogastric grooves present. Hepatic grooves broad and poorly defined. The most prominent grooves on carapace separate gastrocardiac region from branchial regions. Broad grooves separate urogastric, cardiac, and intestinal regions, two faint grooves separate branchial regions into 3 parts, the anterior runs over carapace edge just behind lateral spine then swings rapidly forward toward cervical furrow. Rostrum about ¼ carapace width. Orbits small, upturned, with notch near inner corner, with raised rim. Distance between outer edges of orbits about 50% carapace width. Cephalic arch differentiated into small mesogastric area; large protogastric area surmounted by large, low circular bosses; and an upturned hepatic region with at least 2 small marginal spines immediately ahead of cervical notch. Scapular arch well differentiated into a segmented medial ridge (consisting of urogastric, cardiac, and intestinal regions) and branchial regions (divided into epibranchial, mesobranchial, and

metabranchial regions). Urogastric regions have a gentle forward slope and a steep posterior slope giving rise to 2 transverse crescentic ridges with small medial spine where they meet. Cardiac region diamond-shaped with 2 tubercles symmetrically placed across medial axis. Intestinal region poorly defined and partly missing, a single medial intestinal tubercle near hind margin. Short longitudinal ridges lie in each gastrobranchial groove, perhaps the ridges formed within the epimeral muscle scars. Epibranchial region small but forming the prominent lateral wing of this taxon. A small marginal epigastric spine lies in posterior part of cervical notch. Two small spines are situated near lateral margin of epibranchial wing; the anterior smaller and the posterior larger. Mesobranchial and metabranchial regions with fairly continuous broad longitudinal ridges from near the epibranchial groove to hind margin. Posterior of mesobranchial region with small boss on this ridge, surmounted by several granules. A small marginal spine situated at anterior of metabranchial region. Hind margin missing.

Comparison.—*Hillius youngi* differs from *Orthopsis bonneyi* Carter 1872 by its lack of anterolateral spines, single instead of double orbital lobe, more subdued carapace relief, and different carapace outline due to the widest point of the carapace being farther forward.

Remarks.—The line drawing of the carapace of this taxon is based on a single steinkern. When further material becomes available the description should be amended to include surface ornamentation.

Family Torynommidae Glaessner 1980
Genus *Dioratiopus* Woods 1953

Dioratiopus Woods 1953, p. 52; Wright and Collins 1972, p. 33, 34, 42.
Doratiopus Woods, Glaessner 1969, p. 492 (erroneous spelling).
Glaessneria Wright and Collins 1972 (*non* Takeda and Miyake 1964), p. 34 ff.
Glaessnerella Wright and Collins 1975, p. 441.

Type species.—*Homolopsis spinosa* (Van Straelen 1936), p. 33; Albian of Valcourt France.

Diagnosis.—"Carapace more or less pentagonal with parallel sides, strongly projected frontal area, long rostrum with lateral spines and large shallow indistinct orbits complete above; the sides are vertical and there are traces of a lateral margin anteriorly, but it is normally not sharp or fully developed; the cervical and branchiocardiac furrows are strongly marked; a short oblique furrow runs forward from the outer end of the branchiocardiac and may extend as far as the cervical, delimiting an epibranchial lobe; there is a strong postorbital spine at or just behind the anterolateral angle." (Wright and Collins 1972:34).

Dioratiopus scotti new species
Pl. 1, figs. 6–7; Fig. 8D

Type.—The holotype, a partial carapace steinkern (orig. GAB 27, specimen 1), collected at Jacob's Well, Hays Co., Texas, is deposited in the San Diego Natural History Museum (SDSNH 23642).

Occurrence, sample size, and preservation.—The holotype is the only specimen of this taxon so far collected. It is decortiated carapace steinkern preserving most of the dorsal shield.

Etymology.—For Alan J. Scott, Texas Cretaceous and Holocene paleontologist and stratigrapher.

Description.—Carapace rectangular, longer (partial length 7.9 than wide (partial width 6.8 mm). Cephalic arch moderately convex transversely; scapular arch fairly flat transversely; carapace relatively level longitudinally.

Cervical furrow narrow, deep, and prominent; dorsally parallel to anterior dorsal shield edge, turning inward and backward, then backward for a short distance cutting across medial ridge. Branchiocardiac furrow crosses carapace just behind cervical fur-

row. Furrows parallel to point where cervical furrow bends inward to cross medial ridge, from where branchiocardiac furrow continues backward joining epimeral muscle scars and spliting at point near posterior epimeral muscle scar, 1 part swinging inward crossing medial ridge as a broad, poorly defined groove and other continuing as epimeral muscle scar. Outer arm of epimeral muscle scar loops back inward forming small, flat, oval area. Well-defined branchial furrow splits off epimeral muscle scar near where it begins the loop, proceeds outward and forward to dorsal shield edge.

Rostrum probably triangular, occupying 40% carapace width. Orbits apparently small; with sharply upturned rims, occupying 55% carapace width. Mesogastric area separated from broad, swollen protogastric regions by shallow, distinct groove, narrow anteriorly but rapidly widening at posterior half. Protogastric region with small circular boss situated at center. A row of 12 small granules begins on raised orbital rim and forms an incomplete circle to mesogastric grooves around each protogastric boss. The region lying between 2 transverse grooves, crescent-shaped, concave side anterior, with short transverse base posterior to middle, giving rise to 2 transverse ridges. Medial area behind, where the second groove crosses, a raised region separated by a shallow medial groove at its summit into 2 longitudinal ridges. Rear portion of dorsal shield missing. Branchial regions divided into 2 parts by branchial cardiac furrows running forward and outward; anterior region has single longitudinally expanded granule near outer edge, posterior branchial region has 2 granules on outer margin directly behind 1 on the anterior branchial lobe. The anterior of these 2 is longitudinally expanded and large; the posterior round and small.

Margins of dorsal shield poorly preserved. The photograph, taken before preparation was finished, gives the impression of a straight lateral margin (left side) nearly to a point on line with the rear of the orbits. The right side appears to be gently convex.

Comparison.—*Dioratiopus scotti* is most similar to *D. spinosa* (Van Straelen 1936) in the size and shape of carapace regions. It differs from *D. spinosa* by having a wider urogastric region with 2 transverse ridges, a longitudinally bilobate cardiac region, apparently no furrow delimiting an epigastric region, distal spines on the branchial regions, and probably a smoother carapace. The differences in carapace size and shape, size, shape, and arrangement of carapace regions, and ornamentation is even greater between *D. scotti* and other congeners.

Remarks.—The placement of this single specimen into generic level taxon is strongly hampered by its mode of preservation as a steinkern and by the obscure nature of the lateral margins of the carapace fragment. The discontinuous nature of the lateral margins may point to the lack of dorsal pleural sutures, *linea homolica,* in which case this specimen does not belong in *Homolopsis.* This lack of a straight break and the similarity of carapace morphology to *Dioratiopus* suggests a close alliance with this genus, and the specimen is therefore assigned to *Dioratiopus* until more complete material becomes available.

Section Oxystomata H. Milne-Edwards 1834
Superfamily Calappoidea de Haan 1833
Family Calappidae de Haan 1833
Subfamily Necrocarcininae Förster 1968
Genus *Pseudonecrocarcinus* Förster 1968

Type species.—By monotypy; *Necrocarcinus quadriscissus* Noetling 1881, p. 368, pl. 20, fig. 4); Maastrichtian, Limbourg, Holland.

Diagnosis.—Carapace wider than long, frontal-orbital margin about ½ carapace width. Medial regions poorly differentiated. Mesogastric and protogastric regions combined into wing-like swellings. Inner side of epibranchial region with ridge, outer side with tubercle groups; metabranchial region with weak longitudinal ridges. Sulcus of rostrum with 2 or 4 pits. Deeply incised angular grooves form the lateral boundaries of the urogastric region.

Pseudonecrocarcinus stenzeli new species
Pl. 1, figs. 3–5; Fig. 8B

Types.—The Holotype, an impression of a carapace, (orig. GAB 25, specimen 8) is deposited in the San Diego Natural History Museum (SDSNH 23641).

Occurrence, sample size, and preservation.—The Holotype, an impression, and 5 partial carapaces were collected at GAB 25.

Etymology.—Named in honor of Dr. Henryk B. Stenzel, a leader in the study of Cretaceous and Tertiary Texas decapods.

Description.—Carapace slightly wider than long; widest about ⅓ distance from front. Length from broken tip of rostrum to hind margin 11.8 mm and width (computed as 2 times the width of half the crab) 12.5 mm.

Carapace fairly flat transversely and longitudinally, anterolateral margins lie lower than gastric arch. Cervical furrow broad, faint distally but narrower and more distinct on central part of carapace near where it ends in a pair of gastric pits; branching at distal end, 1 branch continues laterally to dorsal shield edge and other swings anteriorly forming a broad, shallow depression which borders anterior side of hepatic region, arched orbital region, and arched protogastric region. Epimeral muscle scars deep, forming the most noticeable grooves. Inner side of V's thus formed continue forward as shallow, broad depressions connecting with cervical furrow; very faint grooves separate mesogastric and protogastric regions.

Carapace regions poorly differentiated by shallow grooves; separation into bosses or areoles similarly subdued. Rostrum broad, nearly 25% carapace width. Orbits large, arched upward, 2 fissures on rear margins, width between outer edges of orbits about 50% carapace width. Mesogastric and protogastric regions barely discernable. Two pairs of pits lie behind rostrum in mesogastric–protogastric grooves on line with back of supraorbital fissures; outermost pair larger, situated slightly more forward than smaller, better–defined pair. Protogastric regions with broad, poorly defined bosses. Hepatic region with raised boss directly above anterolateral spine. Cardiac regions sharply set off from branchial regions by epimeral muscle scar but barely separated anteriorly except for shallow cervical groove, continuing posteriorly with intestinal regions to hind margin. Branchial regions broadly arched near epimeral muscle scars, with a raised ridge along carapace edge from just behind cervical furrow to a point on line with middle part of epimeral muscle scar.

Anterolateral margin slightly concave for a short distance as it leaves protruding outer edge of orbit, dropping in elevation until it begins to become convex, arching slightly upward then downward just in front of hepatic spines. Indentations in carapace margin in front of hepatic spine and behind it where cervical furrow meets carapace edge. Posterolateral margin slightly convex from cervical furrow to hind margin. Hind margin concave, bordered by shallow but distinct groove.

Carapace ornamentation consists of the few broad bosses, anterodistal branchial ridges, deep epimeral muscle scar, shallow grooves, and a very fine granulation (slightly coarser on medial part) over carapace.

Comparison.—The genus *Pseudonecrocarcinus* contains *P. quadriscissus* (Noetling 1881), *P. biscissus* Wright and Collins 1972, and *P. stenzeli* Bishop new species. All 3 species have post-rostral pits in common. This character separates this genus from the other genera of the Necrocarcininae. In *Pseudonecrocarcinus stenzeli* and *P. quadriscissus* the pits are elongated into slits. The carapace of *P. stenzeli* is much smoother than that of *P. quadriscissus.*

Remarks.—The presence of pits at the base of the rostrum unite *P. quadriscissus, P. biscissus,* and *P. stenzeli* into a distinct group. I believe it is best to maintain their distinction as a separate genus until such time as we have more data with which to judge the phylogenetic affinities of the necrocarcinids.

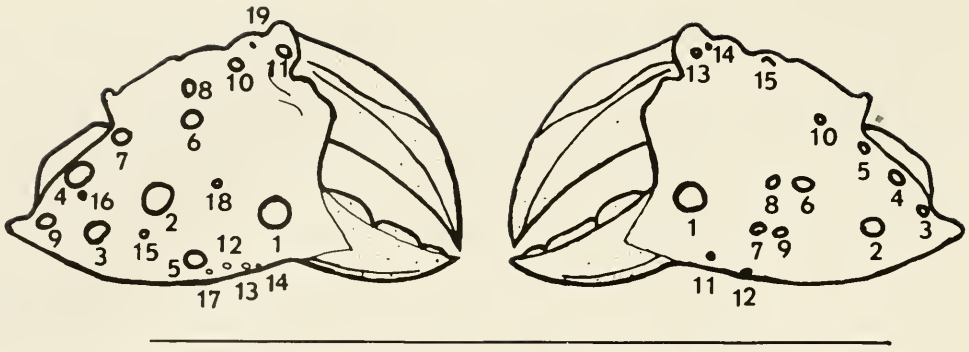

FIGURE 11. Tubercle placement on claws of *Prehepatus hodgesi* Bishop.

Superfamily Calappoidea de Haan 1833
Family Calappidae de Haan 1833
Subfamily Matutinae McLeay 1838
Genus *Prehepatus* Rathbun 1935

Type species.—By original designation: *Prehepatus cretaceous* Rathbun 1935, p. 47, Pl. 11, figs. 29–30.

Diagnosis.—Chelae small, increasing in height to distal end of palm; fixed finger short, movable finger stout; transversely flat to concave on inner face, convex on outer face with upper margin broadly rounded to flat and forming an oblique keel which overhangs the inner face; surface ornamented by strong tubercles.

Prehepatus hodgesi new species
Pl. 3, figs. 1–19; Figs. 8F, 11, 12; Tab. 7

Types.—The holotype of *Prehepatus hodgesi* is a partial right propodus (orig. GAB 25, specimen 14) deposited in the San Diego Natural History Museum (SDSNH 23655). Six paratypes (SDSNH 23656 to 23661) are also deposited in the San Diego Natural History Museum.

Occurrence, sample size, and preservation.—Twenty claws of this taxon are known from localities GAB 21, GAB 25, and GAB 26.

Etymology.—Named in honor of Floyd Hodges whose fortuitous spilling of coffee on his lap caused the discovery of the Boerne-Sisterdale locality (GAB 25) which yielded so many fine specimens of this taxon.

Description.—Carpus with large tubercle on rear distal corner, smaller tubercle on front distal corner, 1 on center of dorsal face and 1 midway on rear dorsal margin. Margin of proximal, dorsal side with row of 5 granules.

Right propodus triangular, about twice as long as high (Table 7), palms slightly longer than high, highest at distal end of palm. Level upper margin about half the length of convex lower margin, flat, horizontally overhanging inner face at proximal edge. Carinate proximal part of crest gives way to 4 broad, thin blade–like spines which become progressively more vertical distally to base of dactylus. Lower margin transversely convex. Outer face convex longitudinally, very convex transversely. Inner face fairly flat. Two broad, shallow concavities present, 1 below upper margin and 1 at proximal end just above lower margin. Propodus ornamented by numerous tubercles (situated in 3 lines). Upper sinuous row of 6 tubercles (9, 7, 8, 10, 11) beginning at lower carpal articulator follows the carpal margin, swinging forward to follow the upper margin to distal edge above dactyl articulator. Second row begins at same point as first (near lower carpal articulator), proceeds in sinuous path to base of fixed finger through 4 large tubercles (counting the first one again) (9, 3, 2, 1) and 1 minor tubercle (18) between distal 2 tubercles (1 and 2). The distal 3 tubercles of this row are the most

TABLE 7. Measurements in millimeters of right claws of *Prehepatus hodgesi*. * = average size, + = very large, − = smaller than average, ? = cannot tell because of preservation. H = claw height, Lpm = claw length without fixed finger, Lpd = length with fixed finger.

Specimen	H (mm)	Lpm (mm)	Lpd (mm)	Tubercle 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Right Claws‡																						
25–13 cp	4.7	6.75		*	*	*	*	–	–		–	*	*			*	*		?	*		
SDNHM 23655 (=25–14) p	5.25	7.3		*	*	*	*	*	*	*	*	*			*	*	*	*	*	*		
SDNHM 23657 (=25–16) p	4.44	5.87		*	?	?	?	?	?	*	?	?	?	?	?	?	?	?	?	?	?	?
25–17 cp	3.94	5.62		*	*	*	*	*	–	*	*	–	*			*	*			*		*
25–32 p	6.76	8.59		*	*	*	*	*	–	*	*	*	–	*		*						*
25–33 p	3.47	4.32		–	–		–			–	–	–	–									
25–34 p	3.59	4.79		–	–	–				–												
25–35 p	4.40	6.62	7.98	*	*	–	*	–	*	*	*	*	*	*								*
25–36 pd	4.82	6.21	8.22	*	–	–	–					–										
25–37 p	4.16			*	*	–	?	–		?	?	?	?	?	–	–						?
25–38 cp	4.37	5.77		*	*	–	+	–		*					*						+	
25–39 cp	4.24	6.21		*	*	–	*	–	–	–	–	–			–					–		
25–40 cp	4.80	5.90		*	*	*	*		–	*	?	–	*		*	?	*	*				
25–41 p	5.48	7.73	8.19+	*	*	–	–	–	?	?		–	?	?		–						
25–20 cp	5.51	7.95		*	*	*	*			–	–	–	?	?								
25–21 cp	2.84	3.88		*			–			–	–	?										
25–45 p	3.66	4.91		?	?	?	?															
25–47 p	6.82	9.57		*	*	*	*	*	*		*	?	*	*	*	*						
25–48 cp	4.25			+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SDNHM 23659 (=21–22) pd	3.56	4.99	6.46	*	*	*						*	?				–				+	
Left Claws‡																						
25–42 cp	2.73	3.50		*		?	–	–	–				–									
25–44 cp	4.28	5.72		+	*		*	*	*				–	–		–	–	–				
25–43 p	4.84	6.26		+	–	–	*	–	*				–	–	–							
SDNHM 23661 (=25–15) p	5.97	8.55		+	*	*	*	*	*	*	*											
25–46 p	5.11+	7.31+	10.06+	+	*	*	*	*	*	*		*	?									
25–49 cp	5.83	7.81		*	*	*	*	*	*	*				*	*?	*		*				
25–50 p	5.4	7.9		*	*	*	*	*	*				*			–	–	+				
25–51 p																						

‡ c = carpus present, p = propodus present.
pd = ?

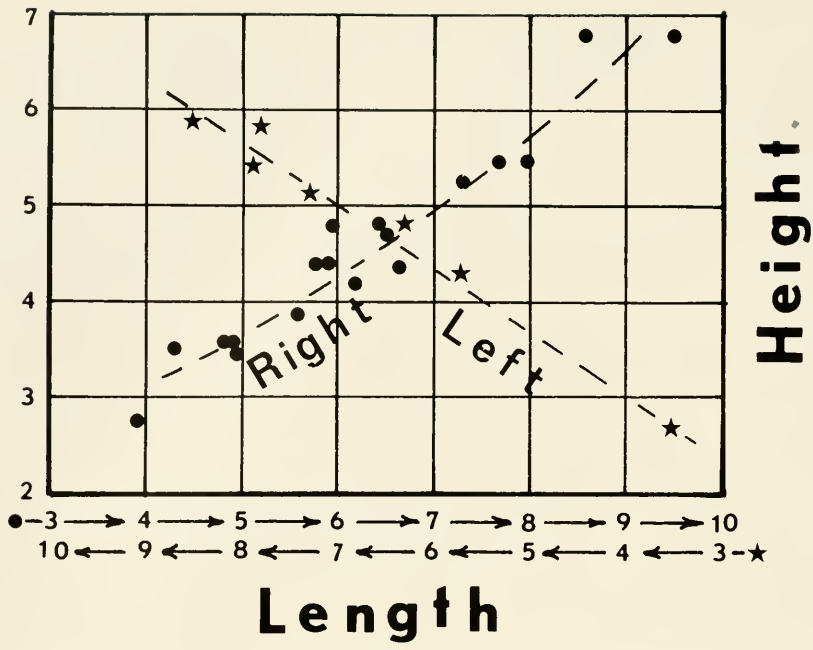

FIGURE 12. Graph of palm height (mm) vs. palm length (mm) for *Prehepatus hodgesi* Bishop. Right claws plotted as dots (read length on top scale increasing left to right) and left claws as stars (read length on lower scale increasing from right to left).

consistent of the tubercles in presence and relative size. A third row of tubercles (5, 12, 13, 14) runs in a straight line from a medium tubercle (5) above midpoint of lower margin almost to lower edge of the fixed finger. In addition to these "rows" a small node is sometimes found in angle formed by the upper rows (16), a medium tubercle (6) below middle of upper row, a small one (15) below and behind tubercle 2, a small one (17) below tubercle 5, and a small one (19) above and between tubercles 10 and 11. A spot above tubercle 8 sometimes is roughened or tuberculate. Inner face ornamented by a single tubercle midway along carpal margin. Fixed finger turned downward and slightly inward, with faint furrow on lower edge of outer face. At least 2 "teeth" are present on prehensile edge; proximal tooth's surface divided into 3 lobes. Movable finger strongly curved, with narrow angular ridge on outer side from the articulator to midway along dactyl, where it broadens and rounds out to tip. Fingers finely granulate and weathered differently than rest of claw, appearing more stable or resistant.

Left propodus same shape as right, probably also same size (Table 7), outer surface with fewer tubercles than right. Tubercle size highly variable, positions more variable than those on right claw. A row of 4 tubercles (3, 4, 5, 10) runs in an arc along carpal margin from lower articular onto palm. Most other tubercles lie on 2 lines that run between major tubercle (1) at base of fixed finger to a large spine (2) distal of lower carpal articulator, upper row convex upwards, consisting of 4 tubercles (1, 8, 6, and 2), lower row convex downward and consisting of 4 tubercles (1, 7, 9 and 2). Two small tubercles (11 and 12) may be situated on lower edge of palm below tubercles 1 and 7. Three small tubercles (13, 14, and 15) may be present on flattened crest.

Comparison.—*Prehepatus hodgesi* has a consistent (though variable) pattern of tuberculation different than *P. cretaceus* Rathbun 1935; *P. pawpawensis* Rathbun 1935; and *P. dilksi* Roberts 1962. *Prehepatus hodgesi* is not as rectangular as *P. cretaceus* Rathbun 1935, lacks the great number of spines on the upper margin, does not possess the large tubercle near the upper dactyl articulator, and does not have a tuberculate dactylus.

Prehepatus hodgesi does not have the numerous fine granules of *P. pawpawensis.*

TABLE 8. Measurements in millimeters of claws of *Torynomma? densus*.

Specimen	Palm length (mm)	Height (mm)	Claw length (mm)	Claw thickness (mm)
SDNHM 23664 (=25–5)	7.5	7.0	12.3	3.8
SDNHM 23663 (=25–10)	7.2	5.8		

Prehepatus hodgesi differs from *P. dilksi* Roberts 1962 in its ornamentation, lack of granulate dactylus, and lack of the vertical furrow and rim on the propodus along the distal end of the outer surface.

Remarks.—The taxon shows a surprisingly consistent pattern of ornamentation in the arrangement of tubercles and an equally surprising amount of variation in size (or presence) of the tubercles. If only a few specimens had been found, it is quite probable I would have been tempted to place them in different species level taxa.

I feel fairly confident that there are at least 2 recognizable instars. The smaller specimens are relatively thinner and nearly smooth. A second instar shows tremendous variation in tubercle size. A third possible instar may be present and contains the largest, most-ornamented specimens.

The data on cheliped ornamentation are included as I believe there may be a behavioral analogy with the claws of fiddler crabs (Crane 1975) and the data may be useful to subsequent decapod workers.

Section Brachyrhyncha Borradaile 1907
Superfamily Dorippoidea de Haan 1841
Family Dorippidae de Haan 1841
Genus *Torynomma* Woods 1953

Type species.—*Torynomma quadrata* by original designation.

Diagnosis.—"Carapace subquadrate, widest anteriorly, orbital grooves large, rostrum narrow, oviduct opening on coxa of 3rd periopods." (Glaessner 1969:493.)

Torynomma? densus new species
Pl. 3, fig. 32–40; Fig. 8J; Tab. 8

Types.—The Holotype, a right propodus (GAB 25, specimen 5) and paratype (GAB 25, specimen 10) are deposited in the San Diego Natural History Museum (SDSNH 23664 and SDSNH 23663 respectively).

Occurrence, sample size, and preservation.—*Torynomma? densus* is represented by 2 right propodi from GAB 25. The holotype is nearly complete except for some dissolution of exoskeleton. The paratype is partly crushed on the inner side and has the fixed finger broken off. Neither specimen preserves the dactylus. The band of dense exoskeleton along the distal margin and on the fixed finger is excellently preserved on each specimen.

Etymology.—For dense exoskeleton along distal edge of claw.

Description.—Claw nearly twice as long as high, palm slightly longer than high. Lower margin slightly convex, tightly rounded at lower proximal corner slanting forward along carpal articulation, then broadly rounded to convex upper margin. Distal edge nearly vertical concave to base of fixed finger. Fixed finger long, narrow, curving inward; decreasing in size distally by 2 steps before it reaches pointed tip. Outer face of claw convex, inner face slightly convex. A band of dense exoskeleton present along distal edge of claw and on fixed finger.

Shallow depression on outer face on dense band at base of upper margin of fixed finger, giving way to shallow groove that parallels lower margin of finger to its tip. Field of small granules near the upper part of dense band and below fixed finger groove. A smooth lineation lies on the lower edge of the claw giving rise to an apparent groove. Knob-shaped upper carpal articulator granulate.

Inner face fairly flat, shallow depression below upper margin forming slight overhanging ridge, coarsely granulate on dense band. A shallow, smooth groove running along middle of finger joins second step-down. Dense band abundantly granulate below groove and sparsely granulate above it. A field of numerous granules lies on the dense band even with upper margin of fixed finger. Occlusional surface formed by a broad ridge with 2 "teeth" formed where the step-downs in size occur.

Comparison.—*Torynomma? densus* has a shape similar to *Torynomma quadrata* Woods 1953 but differs by a more convex lower margin, a stouter, stepped-down fixed finger, and the band of very dense exoskeleton on the fixed finger and along the distal edge of the palm.

Remarks.—The assignment of this claw to a taxon was most difficult because most taxa that have a preserved carapace do not have an adequate description of the chelae. The dense exoskeleton on the finger and distal edge of the claw suggests that this may be a xanthid-like crab. It was not assigned to the Xanthidae because on xanthids usually only the fingers have dense exoskeleton, the fixed finger in xanthids normally has "teeth," and this taxon would have extended the range of xanthids from Upper Cretaceous into the Lower Cretaceous.

It was deemed better in this case to name a new taxon (knowing it will most likely be synonomized when the claw is matched to a carapace) than to have yet another nameless taxon to refer to in the literature.

Acknowledgments

Many persons were directly or indirectly involved in this study. Those who aided by helping collect specimens were Nelda Bishop, Susan Deutsch Conger, Arthur Cleaves, Lyman Dawe, Tom Grimshaw, Floyd Hodges, Don Lentzen, John Newcomb, Mary Beth Bowers Schwartz, and Keith Young. Discussions with Keith Young, H. B. Roberts, Alan Scott, and particularly Peter Rodda resulted in a stimulus to complete this study. The manuscript was reviewed by Rodney Feldmann and Karl Waage. Jacque Causey typed the final manuscript at Georgia Southern College. A Faculty Research Grant from the Faculty Research Committee, Georgia Southern College, expedited the completion of this work, and an NSF grant (DEB 8011570) provided time for major revision and publication costs.

Literature cited

Bell, T. 1850. Notes on the Crustacea of the Chalk formation, *in* F. Dixon (editor) The geology and fossils of the Tertiary and Cretaceous formations of Sussex. Longman, Brown, Green and Longmans, London, England.

Bell, T. 1858. A monograph of the fossil malacostracous Crustacea of Great Britain. Pt. I. Crustacea of the London Clay, pages 1–44. Palaeontograph. Soc. London.

Bell, T. 1863. A monograph of the fossil malacostracous Crustacea of Great Britain. Pt. II Crustacea of the Gault and Greensand, pages 1–40. Palaeontograph. Soc. London.

Carter, J. 1872. On *Orithopsis boneyi,* a new fossil crustacean. Geol. Mag. 9:529–532.

Crane, J. 1975. Fiddler crabs of the world. Princeton University Press, Princeton, N. J., USA.

Förster, R. 1968. *Paranecrocarcinus libanoticus* n. sp. (Decapoda) und die Entwicklung der Calappidae in der Kreide. Mitt. Bayer. Staatssamml. Palaont. Hist. Geol. 8:167–195.

Glaessner, M. F. 1969. Decapoda. Pages 399–651 *in* R. C. Moore (editor). Treatise on invertebrate paleontology. Geol. Soc. Amer. and Univ. Kans. Press, Lawrence, Kansas, USA.

Hendricks, L., and W. F. Wilson, 1967. Comanchean (Lower Cretaceous) stratigraphy and paleontology of Texas. Permian Basin Section Soc. Econ. Paleont. Min., Pub. No. 67-8.

Noetling, F. 1881. Ueber einige Brachyuren aus dem Senon von Maestricht und dem Tertiar Norddeutschlands. Deutsch. Geol. Gesell. Zeitschr. 33:357–371.

Rathbun, M. J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. Geol. Soc. Am. Special Paper 2.

Roberts, H. B. 1962. Crustacea. Pages 163–191, *in* H. G. Richards et al. (editors). The Cretaceous fossils of New Jersey: New Jersey Bur. Geol. and Top. Paleont. Ser., Bulletin 61, Trenton, N.J., USA.

Stenzel, H. B. 1945. Decapod Crustacea from the Cretaceous of Texas. Texas Univ., Publ. No. 4401:401–476.

Stimpson, W. 1859. Notes on North American Crustacea. N.Y. Lyc. Nat. Hist., Ann. 7:53.

Stricklin, F. L., Jr., C. I. Smith, and F. E. Lozo, 1971. Stratigraphy of Lower Cretaceous Trinity Deposits of Central Texas. Tex. Bur. Econ. Geol. Rept. Invest. 71:1–63.

Van Straelen, V. 1936*a*. Contribution à l'étude des crustaces décapodes de la periode jurassique. Mém. Acac. r. Belg. Cl. Sci. 7:1–462.

———. 1936*b*. Crustaces décapodes nouveaux ou peu connus de l'époque crétacique. Bull. Mus. R. Hist. Nat. Belg. 12(45):1–50.

Winter, J. A. 1962. Fredricksburg and Washita strata (Subsurface and Lower Cretaceous) Southwest Texas. Pages 81–115, *in* Contrib. Geol. So. Tex. The South Tex. Geol. Soc.

Wright, C. W., and J. S. H. Collins, 1972. British Cretaceous Crabs. Palaeontographical Soc. (Monograph).

Wright, C. W., and J. S. H. Collins, 1975. *Glaessnerella* (Crustacea Decapoda, Cymonomidae), A replacement name for *Glaessneria* Wright and Collins, 1972 *non* Takeda and Miyake, 1969. Palaeontology. 18:441.

Young, K. P. 1972. Cretaceous paleogeography, Implications of endemic ammonite faunas. Tex. Bur. Econ. Geol. Circ. 72-2:1–13.

Young, K. P. 1974. Lower Albian and Aptian (Cretaceous) Ammonites of Texas. Geoscience and Man. 8:1–175–228.

TRANSACTIONS
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A new subspecies of *Euphyes vestris* (Boisduval) from southern California (Lepidoptera: Hesperiidae)

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Abstract. *Euphyes vestris harbisoni*, from southern California, is described and illustrated. This subspecies is phenotypically distinct and geographically isolated from all other populations of *E. vestris* (Boisduval). Its range is restricted in part by the distribution of the larval host plant, *Carex spissa* Bailey (Cyperaceae). Life history data are presented including descriptions of the immature stages. Additionally, *E. ruricola* (Boisduval) is removed from the synonymy of *E. vestris*.

Introduction

Euphyes vestris (Boisduval 1852) has long been recognized as a polytypic species, with subjective separation of an eastern population, *Euphyes vestris metacomet* (Harris 1862), from the nominate western population. Additionally, it has been appreciated by some that a phenotypically distinct population of *E. vestris* exists in extreme southern California (Emmel and Emmel 1973). Data available indicate the presence of this insect in scattered populations from Orange County (Orsak 1977) through western San Diego County, with speculative distribution to include the northern mountain ranges of Baja California Norte, México (MacNeill 1962). However, because sampling and study of the southern California population has been extremely limited, definitive analysis had not been previously accomplished and its status remained uncertain. Based on the data herein presented, it is now obvious that the population of *E. vestris* centered in San Diego County, California, represents a morphologically distinct form that is geographically isolated from the nearest *E. vestris* populations both to the north and east. Accordingly, we propose a name for this southwestern population, and report previously unknown life history data.

Depositories abbreviated in the text are as follows: RB, Richard Breedlove, San Diego, California; GB, Guy Bruyea, Poway, California; CS, Chuck Sekerman, North Hollywood, California; LG, Lee Guidry, Point Loma, California; LACM, Los Angeles County Museum of Natural History; SDNHM, San Diego Natural History Museum; CIS, California Insect Survey, University of California, Berkeley; and UCI, University of California, Irvine.

Systematics

Considerable controversy and confusion exist regarding the correct specific name of *Euphyes vestris* (Boisduval). The 2 nominal taxa "*Hesperia*? *vestris*" [sic] and "*Hesperia ruricola*" were described by Boisduval (1852) from specimens collected in California by P. Lorquin. The 2 have become confused largely owing to the loss of the type of *ruricola* (*fide* Oberthür, Evans 1955); the type of *vestris* is reportedly in the British

Museum (Evans 1955). Although *ruricola* has page priority, the absence of type material and the inconclusive nature of the original description have traditionally relegated this taxon to junior synonym of *vestris*. However, Evans (1955) indicates that the description of *ruricola* in "no way" agrees with *vestris*. Furthermore, he maintains that the two taxa are actually in different genera; *ruricola* belonging to the genus *Hesperia* Fabricius, and *vestris* correctly placed in *Euphyes* Scudder. This is supported, in part, by the question mark placed after the genus "*Hesperia*" in Boisduval's original description of *vestris*. The fact that Boisduval questioned the congeneric nature of *vestris* and *ruricola* clearly indicates that these two taxa do not represent the same species. Therefore, Evans was correct in removing *ruricola* from the synonymy of *vestris*. F. M. Brown (1957) states "Holland [(1905)] was responsible for the confusion when he, contrary to most of the evidence and the original description, applied [the name] *ruricola* to the Dun Skipper [*E. vestris*] . . . ."

Miller and Brown (1981) recently revived *E. ruricola* "on the basis of a specimen that might be the type that is labelled as '*ruricola*' in Boisduval's hand . . ." which had been located in the collection of the Carnegie Museum. This specimen was designated as the lectotype in 1976 by Brown, Miller, and Clench, according to the lectotype label (Carnegie Museum lectotype no. 733). This type designation, however, was never published, and the senior author's personal examination of the data accompanying the specimen revealed a single label that could possibly have been written by Boisduval—"Californie (Lorquin)." Contrary to Miller and Brown (1981), there is no evidence to indicate that the specimen in question represents Boisduval's concept of *ruricola*. Since a legitimate holotype of *vestris* exists in the British Museum (Evans 1955), and the description of *ruricola* is obviously not consistent with *vestris*, we propose that *ruricola* be removed from the synonymy of *vestris*.

In agreeing with Stanford (1981) regarding the validity of the subspecific taxon *E. vestris kiowah* (Reakirt 1866), we recognize the following subspecies of *E. vestris*:

Euphyes vestris (Boisduval 1852)
- *E. v. vestris* (Boisduval 1852)
  - (=*Pamphila osceola* Lintner 1878)
  - (=*Pamphila californica* Mabille 1883)
- *E. v. metacomet* (Harris 1862)
  - (=*Pamphila rurea* W. H. Edwards 1862)
  - (=*Hesperia osyka* W. H. Edwards 1867)
- *E. v. kiowah* (Reakirt 1866)

In addition to the above, the distinctive southern California population of *E. vestris* deserves formal recognition. Extensive review of the synonymy has failed to uncover a previous description that could be unequivocally attributed to this southern California population, hence we propose a new name.

Euphyes vestris harbisoni new subspecies
Figures 1–4

Type material.—Holotype male (SDNHM type L-49), 13.3 km east of Dulzura, north slope of Tecate Peak, elevation 500 m, San Diego County, California, 9 June 1981 (J. Brown); allotype (SDNHM type L-50), 13.3 km east of Dulzura, north slope of Tecate Peak, elevation 500 m, San Diego County, California, 14 June 1981 (J. Brown). Paratypes: 18 ♂♂ and 16 ♀♀, same locality as holotype, but dates as follows: 1 ♂, 1 ♀, 28 June 1980; 2 ♂♂, 2 ♀♀, 30 June 1980; 3 ♂♂, 1 ♀, 12 July 1980; 4 ♀♀, 9 June 1981; 4 ♂♂, 2 ♀♀, 14 June 1981; 2 ♂♂, 2 ♀♀, 21 June 1981; 1 ♀, 27 June 1981; 1 ♀, ex-pupa, 2 June 1982; 1 ♀, ex-pupa, 3 June 1982 (all J. Brown); 6 ♂♂, 1♀, 12 June 1982 (L. Guidry).

Disposition of types.—Holotype male and allotype are deposited in the collection of the San Diego Natural History Museum; paratypes distributed among collections of the following institutions: Los Angeles County Museum of Natural History; California Academy of Sciences, San Francisco; United States National Museum of Natural His-

FIGURE 1. *Euphyes vestris harbisoni*, new subspecies, ♂, dorsal, 13.3 km east of Dulzura, San Diego County, California, 12 June 1980.

FIGURE 2. *Euphyes vestris harbisoni*, new subspecies, ♂, ventral, 13.3 km east of Dulzura, San Diego County, California, 12 June 1980.

FIGURE 3. *Euphyes vestris harbisoni*, new subspecies, ♀, dorsal, 13.3 km east of Dulzura, San Diego County, California, 6 June 1981.

FIGURE 4. *Euphyes vestris harbisoni*, new subspecies, ♀, ventral, 13.3 km east of Dulzura, San Diego County, California, 6 June 1981.

tory, Washington, D. C.; Allyn Museum of Entomology, Sarasota, Florida; Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. All remaining paratypes to be retained by the San Diego Natural History Museum.

Additional material examined.—CALIFORNIA: SAN DIEGO COUNTY: No further locality, 1 ♂, 5 June 1936, 1 ♀, 12 June 1936 (J. Creelman, RB), 1 ♀, 17 June 1936 (J. Creelman, LACM), 1 ♂, 5 June 1936, 1 ♀, 7 June 1938 (J. Creelman, SDNHM). San Diego, 1 ♂, 4 July 1920 (O. E. Sette, LACM). San Diego City, 1 ♂, 1 ♀, 14 June 1936 (J. Creelman, LACM). Adobe Falls, 2 ♂♂, 1 ♀, 13 June 1936 (F. Thorne, SDNHM). Flinn Springs, 1 ♀, 1 June 1939, 1 ♂, 15 June 1939, 6 ♂♂, 1 ♀, 16 June 1939, 2 ♀♀, 18 June 1939 (all W. P. Medlar, SDNHM), 1 ♂, 18 June 1939 (W. P. Medlar, UCI), 8 ♂♂, 5 ♀♀, 18 June 1939 (W. P. Medlar, LACM), 2 ♂♂, 10 June 1980, 1 ♂, 18 June 1981 (all J. Brown, SDNHM). Avocado orchard, Flinn Springs, 1 ♂, ex-pupa, 15 June 1982 (J. Brown, SDNHM). Blossom Valley, 8 km WNW Alpine, 2 ♂♂, 3 ♀♀, 17 June 1940, 2 ♂♂, 29 June 1942 (all F. Thorne, SDNHM). Hellhole Canyon, 1 ♂, 12 July 1954 (M. Kenney, CIS). Lower Hellhole Creek, 1 ♂, 13 June 1981 (Brown and Brown, SDNHM). El Cajon, 2 ♂♂, 29 June 1963 (O. Shields, LACM). El Monte Oaks, 1 ♂, 30 May 1965 (R. Breedlove, RB). 1.6 km W Tecate turn-off, 1 ♂, 30 June 1980 (D. Faulkner, SDNHM). 5 km NW Fallbrook, 1 ♂, 23 May 1981, 1 ♂, ex-pupa, 1 June 1981, 1 ♀, ex-larva, 12 June 1981 (all Brown and Brown, SDNHM). Old Viejas Grade, Poser Mountain, 4 ♂♂, 2 ♀♀, 12 June 1981, 2 ♀♀, 17 June 1981, 2 ♂♂, 26 June 1981 (all J. Brown, SDNHM). Behind San Pasqual Academy, 1 ♂, 30 May 1981 (D. Faulkner, SDNHM), 1 ♀, ex-larva, 30 May 1982 (L. Guidry, LG). Poway Green Valley Truck Trail, 1 ♂, ex-larva, 6 June 1982 (L. Guidry, LG). Poway, 1 ♂, ex-pupa, 15 May 1982 (C. Sekerman, CS). Lake Poway, 1 ♀, ex-pupa, 20 June 1982, 1 ♂, ex-pupa, 27 June 1982, 1 ♂, 28 June

FIGURE 5. Male genitalia of *Euphyes vestris harbisoni*, new subspecies.

FIGURE 6. Male genitalia of nominate *Euphyes vestris*, Plantation, Sonoma County, California, 16 May 1958.

1982, 1 ♀, ex-pupa, 4 July 1982 (all G. Bruyea, GB). ORANGE COUNTY: Silverado Canyon, 1 ♂, 29 June 1972 (C. Sexton, UCI), 2 ♂♂, 8 June 1982 (J. Brown, SDNHM), 2 ♂♂, 1 ♀, 5 June 1982 (C. Sekerman, CS).

Distribution.—Currently known only from San Diego and Orange Counties, California.

Diagnosis.—Male: forewing length $\bar{x}$ = 15.2 mm (range 15.0–16.1 mm). Head, thorax and abdomen dark brown, covered with thin light-brown hairs, much lighter beneath. Palpi whitish with orange-brown terminal segment. Antennae gold-brown, ventral surface of club gold, apiculus brown. Forewings chocolate-brown above, with lustrous orange over-scaling near a bold black stigma. Stigma composed of two oval patches forming an inconspicuously broken black dash. Outer margin of forewing with a very fine light tan fringe. Forewings dull brown below, with basal and distal blackening representing the undersurface of the stigma. Hindwings same color as forewings above,

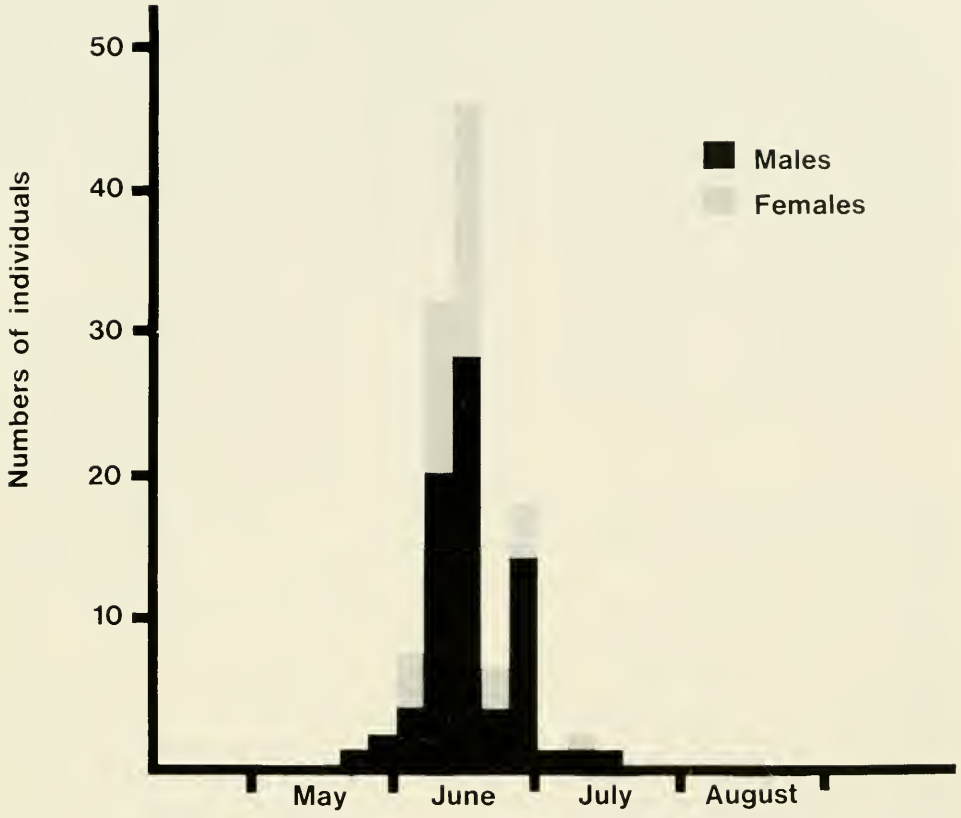

FIGURE 7. Flight period graph of *Euphyes vestris harbisoni*, new subspecies, based on wild caught adults, using all specimens examined.

but with less lustrous orange over-scaling; no additional markings. Hindwings dull brown below, with no markings.

Male genitalia: as illustrated (Fig. 5). The structures of the male genitalia of *E. vestris harbisoni* are very similar to those of both the Arizona populations of *E. vestris kiowah* (not illustrated) and the northern California populations of *E. vestris vestris* (Fig. 6). Compared to nominate *vestris*, the genitalic capsule of *harbisoni* is proportionately longer and slightly less robust, with the valvae more broadly rounded, and lacking the ventral caudal indentation commonly present in nominate *vestris*. The two genitalia figured represent the extremes to more clearly illustrate these differences.

Female: forewing length $\bar{x}$ = 16.0 mm (range 14.7–17.0 mm). As in male except for primary and secondary sex characters. Forewings dark brown above, with lustrous orange over-scaling. Two moderately well-defined hyaline post-median spots just below the discal cell. Females generally with more rounded outer margin of forewing. Forewings dull brown below, with blackening in basal areas slightly more diffuse than in male; the two hyaline spots less well-defined. Hindwings above as in male; dull brown below, occasionally with traces of light spots in the discal band area.

Discussion.—The southern California population of *Euphyes vestris* is single-brooded, the flight period extending from late May through mid-July (Fig. 7). The most distinguishing phenotypic character of the southern California population is its

8

POPULATION STUDIED	NO. ADULTS EXAMINED	MEAN FOREWING LENGTH (mm)	STANDARD DEVIATION	"P" VALUE
Oregon ♂	25	13.524	0.5659	< 0.001
San Diego Co. ♂	40	15.155	0.5296	
Oregon ♀	7	14.000	0.7024	< 0.001
San Diego Co. ♀	22	15.9773	0.6962	
Arizona ♂	30	14.137	0.5648	< 0.001
San Diego Co. ♂	40	15.155	0.5296	
Arizona ♀	19	14.411	0.4736	< 0.001
San Diego Co. ♀	22	15.9773	0.6962	
Arizona ♂	30	14.137	0.5648	< 0.010(NS)
Oregon ♂	25	13.524	0.5659	
Arizona ♀	19	14.411	0.4736	< 0.100(NS)
Oregon ♀	7	14.000	0.7024	

FIGURE 8. Statistical analysis of forewing lengths of various *Euphyes vestris* populations using Student's *T*-test comparing two sample means. "P" value represents the probability that the two samples are homogeneous. "NS" = not statistically significant.

larger size relative to populations from northern California, Oregon and Washington. Its larger size and extensive orange over-scaling clearly distinguish it from the Rocky Mountain *E. vestris* populations, which have been referred to as *E. vestris kiowah* by some authors (Stanford 1981), and the eastern *E. vestris metacomet*. There are some populations of *E. vestris* in Arizona that may be referable to *E. vestris kiowah*, but at this time have not been thoroughly studied. Again, these differ from the southern California population in both size and maculation. An analysis of the male and female forewing measurements between various populations sampled (Fig. 8) demonstrates the statistically significant difference between the San Diego County population and others based on this parameter.

The habitat occupied by the southern California population is remarkably dissimilar to that of all other known populations of *E. vestris*. The southern California population is extremely local, generally occurring in chaparral or riparian communities in narrow canyons where there is a seep or spring providing perennial water (Figs. 9–12); populations found to date have been at elevations below 650 m. The oviposition substrate and larval hostplant is *Carex spissa* Bailey (Cyperaceae), with which the adults are commonly associated (Fig. 13). As indicated by figure 14, *C. spissa* has a limited and spotty distribution from San Luis Obispo County, California, to Baja California Norte, México (Munz 1974). The range of the host plant is obviously a factor limiting the distribution of the butterfly, as supported by the fact that all known populations of *E. vestris harbisoni* (Fig. 15) fall within the range of *C. spissa*. However, factors other than host plant availability must contribute to restrict the insect's range, as indicated by the fact that the butterfly occurs within only a small portion of the host plant's distribution.

Initial observations and efforts to study this insect centered on examination of previously captured material and old collection records. However, there were few previous records for the southern California population of *E. vestris*, and the last specimen collected prior to this study was in 1969 (Stanford *in litt.*). Many prior records came from the Adobe Falls area near San Diego State University, but current development in this area has altered the habitat to the point where it no longer supports the

FIGURE 9. Typical chaparral habitat near Tecate Peak, San Diego County, California.

FIGURE 10. Habitat near Dulzura, California.

FIGURE 11. Seep area at Dulzura locality.

FIGURE 12. Habitat near Dulzura, California.

FIGURE 13. Larval host *Carex spissa* Bailey.

insect. The only recent collections outside of San Diego County were made in the Silverado Canyon area of Orange County (Orsak 1977).

Using prior collection records as a guide, we examined likely habitats in 1980 and 1981 in San Diego County and Baja California Norte. Adult specimens were found first near Flinn Springs County Park, and additional specimens later found in other localities noted above. Fourth instar larvae were subsequently observed 13.3 km east

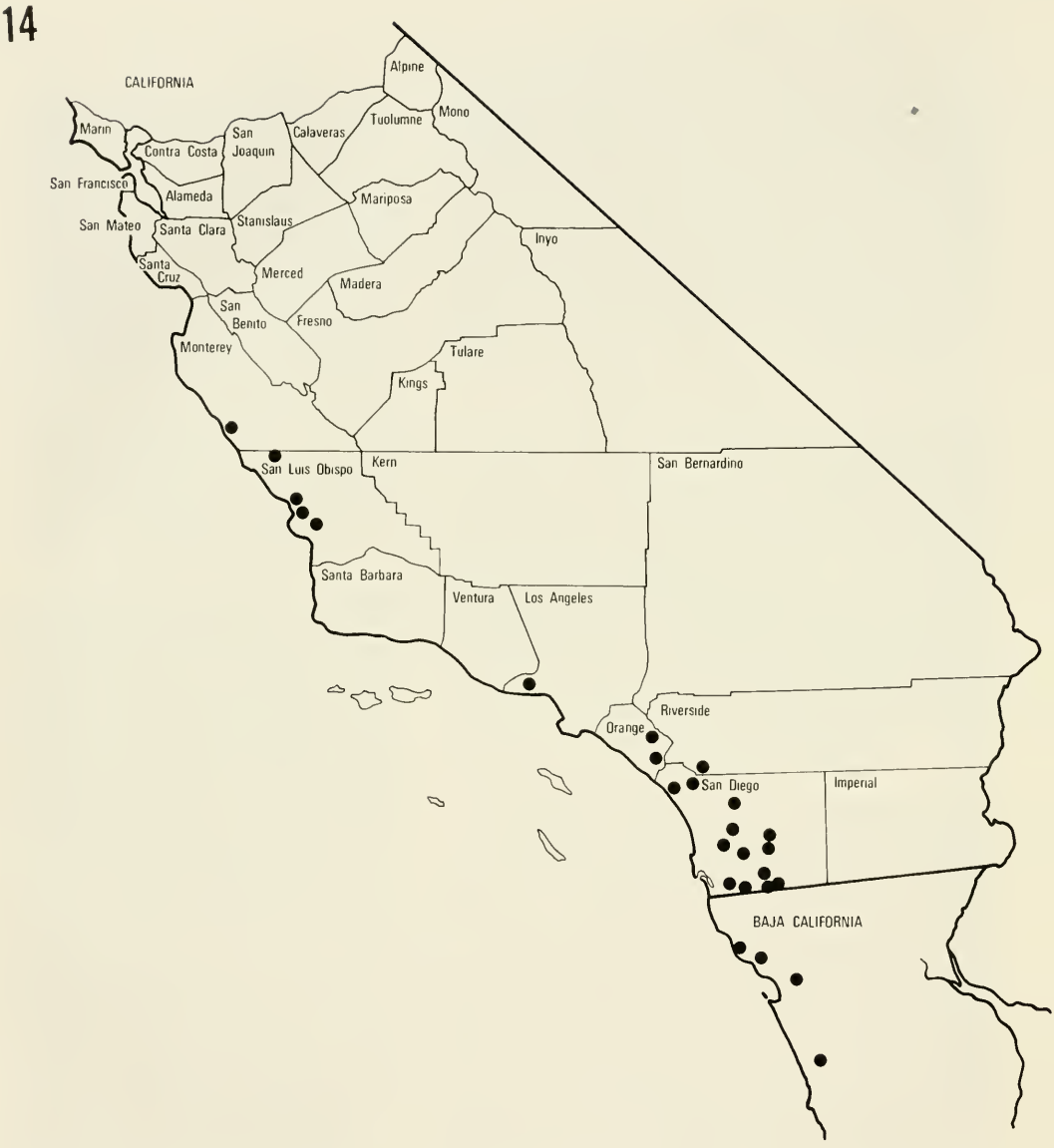

FIGURE 14. Approximate distribution of *Carex spissa* in southern California and adjacent Baja California, Mexico.

of Dulzura in January 1981. All larvae were found in typical hibernacula formed from *C. spissa* (Fig. 16). These hibernacula were formed by the attachment of two, three or four leaves creating a silk-lined, tube-like chamber 7–12 cm long and open at the superior end. The chamber itself is usually located in the superior one-third of the *Carex* leaves. Each leaf or blade is characteristically bent, generally at less than a 100° angle, allowing them to be pulled together and joined with silk by the larva. This type of hibernaculum is fairly characteristic and consistent with previous observations made on other members of this genus, including *E. alabamae* (Lindsey 1923), *E. macguirei* (Freeman 1975), and *E. dukesi* (Lindsey 1923) (William McGuire personal observation).

Etymology.—The subspecies *E. vestris harbisoni* is named in honor of Charles Harbison, Curator Emeritus, San Diego Natural History Museum. Mr. Harbison has been a patient instructor, and enthusiastic field entomologist, and a pioneer in investigating the entomofauna of Baja Californinia, México.

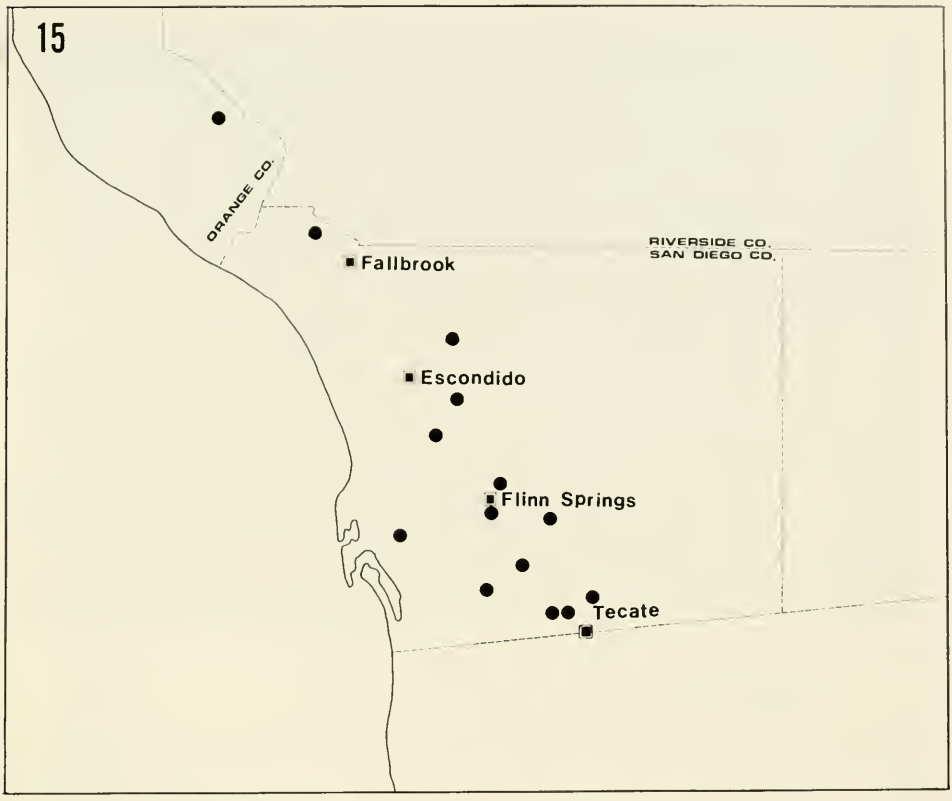

FIGURE 15. Distribution of *Euphyes vestris harbisoni*, new subspecies.

LIFE HISTORY

Early stages.—The early stages of *E. vestris harbisoni* closely resemble those described by Heitzman (1964) for the eastern *E. vestris metacomet*. The larvae of *E. vestris harbisoni*, however, are much larger, and the pupae dark brown rather than green.

Egg.—(Fig. 17). 1.5 mm, hemispherical, pale yellow-green with an irregular red splotch on the apex. An irregular red band encircling the entire egg midway between the base and the apex.

First instar.—Length 7.0 mm. Head: shiny brown. Body: ground color translucent green, abdominal segments 9 and 10 translucent yellow-tan. Several long, fine hairs projecting upwards from the last body segment; thin black collar just behind the head indicating the prothoracic shield.

Second instar.—Length 14.0 mm. Head: yellow-orange with a conspicuous caramel-colored band encircling the head along its outer margins except above the mandibles. Mandibles dark brown. An oblong dark brown spot set vertically in the upper center of the face. Body: ground color translucent green, abdominal segments 9 and 10 translucent, revealing yellow-tan internal organs. Body covered with numerous white setae, several longer thin hairs at end of the last segment. Each spiracle indicated by a fine black dot.

Third instar.—Length 21.0 mm. Head: cream-colored with a well-defined dark caramel-colored longitudinal stripe on each side of the face, and a light brown band extending from the dark spot to the mandibles. Body: ground color translucent green, abdominal segments 9 and 10 more translucent; covered with fine white hairs. Spiracles indicated by a fine black dot.

FIGURE 16. Typical hibernaculum formed from *Carex spissa*. Arrow indicates position of the larva.

Fourth instar.—Length 28.0 mm. Head: caramel-brown with an oblong black spot in the upper center of the face; a narrow cream-colored longitudinal band running parallel to, and on each side of the black spot; a cream-colored band around the outer edge of the jaws. Body: ground color green, with numerous thin white dashes of inconsistent length (previously visible only under microscopy).

Final instar.—(Fig. 18). Length 36.0 mm. Head: caramel-brown with two cream-colored vertical bands; a black oval spot in the upper center of the face. Body: green with extremely thin, wavy longitudinal white dashes. A single, subtle, darker green longitudinal stripe along the center of the dorsal surface. Minute black dots sprinkled over entire body. Terminal abdominal segment translucent pale green. Prothorax white with prothoracic shield indicated by a thin black line running into the enlarged first spiracle dot, forming a thin black wedge. Each spiracle indicated by a black dot, larger for the first and anal spiracles. Ventral surface of abdominal segments 8 and 9 covered with a fine layer of silver-white cottony material.

Pupa.—(Fig. 19). Length 25.0 mm. Dark brown. Abdomen slightly dusted with white cottony material. Most of body covered with short, fine bristles; wing cases bare. Bristles on head and end of abdomen longer. Tongue case long, extending beyond the fourth abdominal segment, lying along the mid-dorsal surface of the pupa, detached above the abdominal segments.

Behavior.—Eggs are laid singly, usually on the undersurface of the leaf blades near the base of the plant. During the first instar the young larvae are generally found along the mid-ridge crease on the upper surface of the leaves, near the base of the plant. The second and third instar larvae, when not feeding, are usually found in silk-lined tubes constructed by the larvae by attaching two to four leaves together longitudinally. It is during the fourth, or occasionally the third instar, that the larvae construct the overwintering hibernacula previously described, and enter a short diapause. The head is always aimed towards the superior end of the hibernacula.

During the last instar the larva consumes the portion of the leaf blades extending beyond the superior end of this hibernaculum. This tube is then abandoned, and the larva moves to a different location on the plant, or to a different plant and constructs a new chamber. The upper portion of these leaf blades are also usually eaten by the

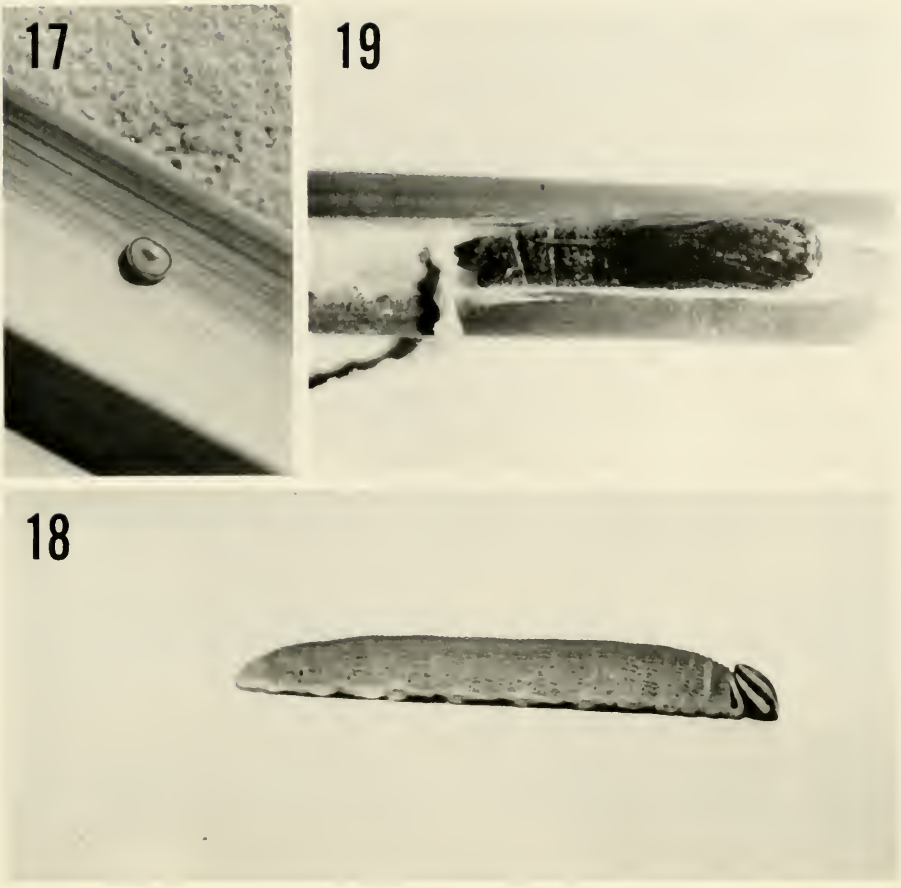

FIGURE 17. Egg of *Euphyes vestris harbisoni*, new subspecies.

FIGURE 18. Last instar larva of *Euphyes vestris harbisoni*, new subspecies.

FIGURE 19. Pupa of *Euphyes vestris harbisoni*, new subspecies.

larva. When a larva is ready to pupate, it fills the upper end of the tube with a flocky, cottony plug 8–10 mm thick. The larva is generally situated in the tube with the head towards the superior end; the pupa is always situated in this manner. Pupation lasts 18 to 21 days.

Adults emerge from late May through June, the flight period extending into early July. At one locality a last instar larva, a pupa, and a single adult were collected on the same day (23 May 1981).

Males commonly "patrol" the canyons, never venturing far from the vicinity of the host plant. Both sexes are avidly attracted to nectar sources which include morning glory (*Calystegia macrostegia tenuifolia* (Abrams) Brummitt), red thistle (*Cirsium occidentale* (Nutt.) Jepson), loosestrife (*Lythrum californicum* T. & G.), and rarely, golden yarrow (*Eriophyllum confertiflorum* (D. C.) Gray) and black mustard (*Brassica nigra* (L.) Kock.). Commonly females are observed perching on the *Carex* and basking in the late morning and early afternoon sun.

CONCLUSION

Euphyes vestris harbisoni is isolated by geography and by the availability of a select host plant. While several of the populations found appear to be stable, all are extraordinarily small. Some of the prior known colonies have been extirpated by construction

projects and other habitat modifications. A search for new populations and extension of range should appropriately be directed into northern Baja California and northward up to and including San Luis Obispo County, thus encompassing the known range of the larval host plant, *Carex spissa*. This search in the projected northern range of the insect is important when considering potential intergradations with the northern California *E. vestris vestris*. *E. vestris harbisoni* appears to be morphologically and biologically distinct, with significant geographic separation from all other known *E. vestris* populations. This restricted range, coupled with the continued threat of habitat degradation as has been demonstrated in the immediate San Diego city area, makes it imperative that careful monitoring be continued.

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Literature Cited

Boisduval, J. A. 1852. Lépidoptères de la Californie. Ann. Soc. Ent. France, ser. 2, 10:315, 317.

Brown, F. M. 1957. Colorado butterflies, part 5. Proc. Denver Mus. Nat. Hist. 7:313.

Emmel, T. C., and J. F. Emmel. 1973. Butterflies of southern California. Nat. Hist. Mus. Los Angeles Co., Sci. Ser. 26:1–148.

Evans, W. H. 1955. A Catalogue of the American Hesperiidae in the British Museum (Natural History), part 4. London, Trustees British Museum. 499 pp.

Heitzman, R. J. 1964. The early stages of *Euphyes vestris*. J. Res. Lepid. 3(3):151–153.

MacNeill, C. D. 1962. A preliminary report on the Hesperiidae of Baja California. Proc. Calif. Acad. Sci. 30(5):91–116.

Miller, L. D. and F. M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. 2:1–280.

Munz, P. A. 1974. A Flora of Southern California. Univ. Calif. Press, Berkeley, Los Angeles, London.

Orsak, L. J. 1977. Butterflies of Orange County, Univ. Calif. Irvine. Mus. Syst. Biol. Res. ser. 4.

Stanford, R. E. 1981. *In* Ferris, C. D., and F. M. Brown (editors). Butterflies of the Rocky Mountain States. Univ. Oklahoma Press, Norman.

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Two new idoteid isopods from Baja California and the Gulf of California (Mexico) and an analysis of the evolutionary history the genus *Colidotea* (Crustacea: Isopoda: Idoteidae)

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Abstract. Two new species of idoteine isopod crustaceans are described from Baja California, *Colidotea wallersteini* new species and *Synidotea francesae* new species (Crustacea: Valvifera: Idoteidae: Idoteinae). The genus *Colidotea* is rediagnosed, a key to the known species presented, and its evolution and historical biogeography described. Both trans-oceanic dispersal and vicariance phenomona appear to have played roles in the establishment of modern distributional patterns of *Colidotea*.

Introduction

The idoteid isopod fauna of the northeast Pacific has, in the past 10 years, come to be quite well known (see Brusca and Wallerstein 1979b for an introduction to the literature). The present study adds 2 new species to this fauna, based on material collected by Dr. D. G. Lindquist (University of North Carolina) and some previously unsorted samples of microcrustaceans at the Allan Hancock Foundation (University of Southern California).

The terminology used in this paper is standard for the idoteid isopod literature (see Menzies 1950 for a summary). The following abbreviations are used: AHF, Allan Hancock Foundation; USNM, National Museum of Natural History; SDNHM, San Diego Natural History Museum.

Systematics

Order Isopoda
Suborder Valvifera
Family Idoteidae
Subfamily Idoteinae

Genus *Synidotea* Harger, 1878

The systematics and biogeography of the genus *Synidotea* were reviewed by Menzies and Miller (1972), who recognized 36 valid species and subspecies, 8 of which occur in California. Iverson (1972) described a ninth species from California (*S. media*). Brusca and Wallerstein (1979a) presented new distributional records for *S. harfordi* Benedict, 1897, which at that time was believed to be the southernmost ranging species of the genus in the northeastern Pacific. They noted its disjunct occurrence: central California to Magdalena Bay (SW Baja California), Mexico, reappearing again in the central Gulf of California, Mexico (2 known records). Brusca and Wallerstein (1979b) reviewed the distributions of the 7 known northeastern Pacific shallow-water *Synidotea*, noting that all but *S. harfordi* were entirely restricted to the cold-temperate waters of the Arctic, Aleutian and Oregonian Provinces. Brusca (in press) discusses phylogenetic

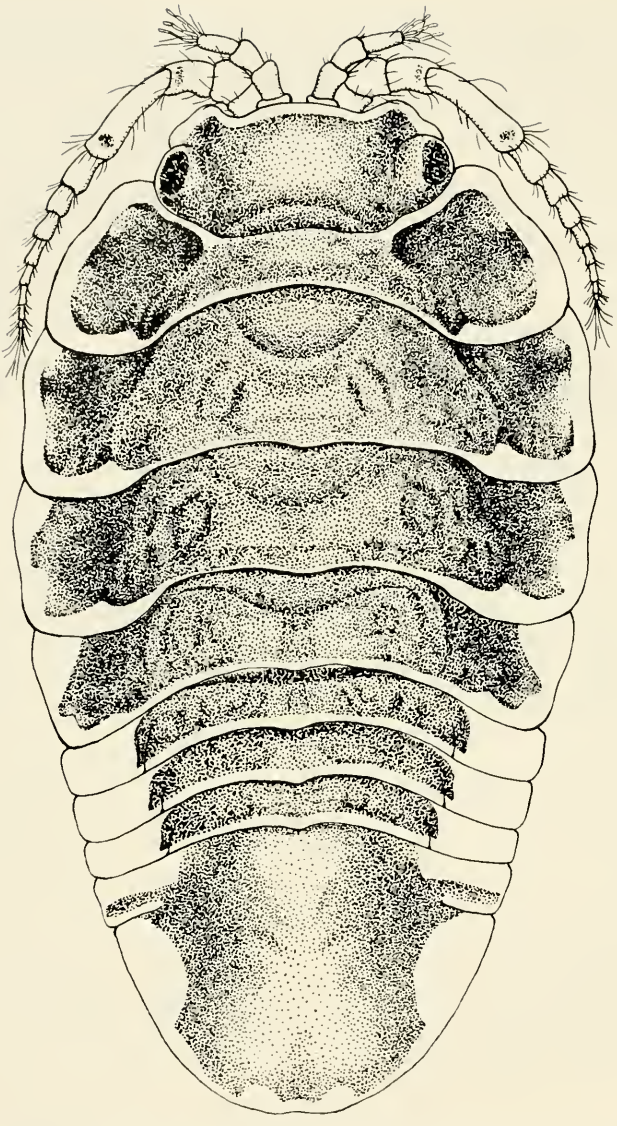

FIGURE 1. *Synidotea francesae* new species. Holotype, AHF 736. Female.

relationships, evolutionary history and zoogeography of *Synidotea,* as well as the 21 other genera of Idoteinae.

Synidotea francesae new species
Figures 1, 2, 3

Types.—Holotype: female, AHF 736; Allotype: male, AHF 736a. Paratypes: 1 female, SDNHM; 1 female, USNM.

Locality.—All specimens from single collection: Mexico, Gulf of California, Sonora, El Golfo de Santa Clara (about 4 miles SE of town); found on sandy beach, "scavenging" on cast up tubes of *Chaetopterus* species (Polychaeta); air temperature 24°C; water temperature (surf) 19°C; 17 April 1973; collected by D. G. Lindquist.

Diagnosis.—Cephalon without horns or other projections; frontal margin convex; eyes bulge outward; body without tubercles or rugae; pleotelson wider than long; per-

FIGURE 2. *Synidotea francesae* new species. Holotype, AHF 736. Female. a, antenna 1. b, antenna 2. c, left mandible. d, lacinia of right mandible. e, maxilla 1. f, maxilla 2. g, maxilliped. h, pereopod I. i, pereiopod IV. j, pereopod VII. k, uropod.

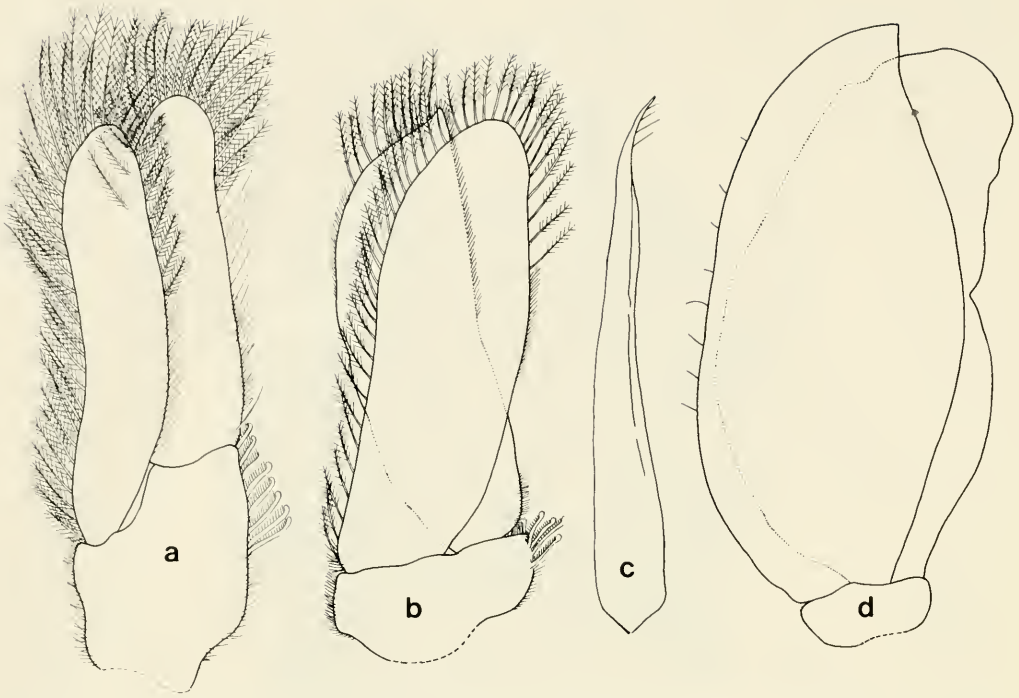

FIGURE 3. *Synidotea francesae* new species. a, pleopod 1 (holotype). b, pleopod 2 (holotype). c, appendix masculinum of pleopod 2, male (allotype). d, pleopod 5 (holotype).

eonites V–VII manifestly shorter than I–IV; median dorsal pattern rounded, as in *S. laticauda*; dorsum with heavy pigmentation.

Description.—Length to at least 6 mm; body ovate and darkly pigmented; dorsum smooth.

Cephalon: Lacking horns or other projections; frontal margin convex, although anterolateral angles somewhat expanded; eyes elevated, on distinct bulges. Antenna 1 with tri-articulate peduncle and uniarticulate flagellum; distal third of terminal article with simple setae and esthetases. Antenna 2 with 5-articulate peduncle and 8-articulate flagellum; all articles with setae; articles 4 and 5 of peduncle each with distinct distal patch of chromatophores; flagellum quite short, extended only to pereonite II. Maxilliped typical for the genus, with single coupling hook. Maxilla 1 typical for the genus; inner lobe with 2 stout plumose setae; outer lobe with 6 long simple setae and 4 short pectinate setae. Maxilla 2 typical for the genus, with plumose, simple and comb setae as figured. Mandible with 4-toothed incisor and large molar process, the latter smooth on outer margin and toothed on inner margin; lacinia mobilis of left mandible 3-toothed; lacinia of right mandible 3-toothed but with additional large serrate spinelike process.

Pereon: Manifestly elevated along middorsal line; entire dorsal surface with dark pigmentation, except along lateral margins. Pereonites I–IV large, long and without dorsal coxal plates; pereonites V–VII small, short, and with large dorsal coxal plates, visible in dorsal aspect by presence of faint suture lines just median of edge of chromatophore pattern; all pereopods form ventral coxal plates that meet in midline of sterna. Median dorsal pattern of pereonites II–IV (*sensu* Menzies and Miller 1972) with rounded posterior margins. Pereonites IV–VII slightly produced along posteromedial margin. Pereopod I with dactyl nearly as long as propodus.

Pleon: Posterior border with faint indentation, otherwise evenly convex. Pleon (=pleotelson) width equal to length, or up to 1.5 times wider than long. Pleopods 1–3

TABLE 1. Principal attributes distinguishing *Colidotea* and its sister-group, *Synisoma*, from each other and from all other genera of Idoteinae.*

	Colidotea	*Synisoma*
Flagella of second antennae	multiarticulate	multiarticulate
Number of articles in maxillipedal palp	4	4
Appendix masculina (of male)	long, arising from base of endopod (of second pleopod)	long, arising from base of endopod (of second pleopod)
Lacinia mobilis	very large; as large or nearly as large as incisor process	very large; as large or nearly as large as incisor process
Pleon	relatively short; much less than ⅓ total body length	relatively long; ⅓ or more total body length
Pleomere fusion	all pleomeres fused; one pair lateral incisions present	all pleomeres fused; no lateral incisions remain
Eyes	very small (except in *C. findleyi*); set on lateral margins of cephalon	very small; set on lateral margins of cephalon

* For comparable data on the other 20 genera of Idoteinae see Brusca (in press).

with plumose marginal setae, decreasing posteriorward; pleopods 4–5 without plumose marginal setae. Uropod with 3 stout plumose setae at junction of protopod and lamella. Appendix masculinum of male simple, with weakly grooved inner margin and a few distal setae; penes entirely fused into large tongue-like flap.

Etymology.—*Synidotea francesae* is named in honor of Frances Runyan: biological illustrator, horticulturist, and friend.

Discussion.—*Synidotea francesae* is similar to *S. laticauda* Benedict, 1897, and *S. harfordi* Benedict, 1897 (both known from California shores), in having a smooth dorsum with a characteristic medial dorsal pattern, evenly convex lateral margins on the body somites, elevated (bulging) eyes, and notch at the apex of an otherwise evenly convex pleotelson. It differs most strikingly from these species in having a pleon as wide or wider than long, a barely perceptable notch at the pleotelson apex (rather than a deep notch), pereonites V–VII manifestly reduced in size, and a distinct dorsal chromatophore pattern. It differs further from *S. laticauda* in having an evenly convex frontal margin, a 4-toothed incisor on the mandible, and shorter antennae. It differs further from *S. harfordi* in having rounded posterior margins on the medial dorsal pattern of pereonites II–IV, shorter antennae, and a coupling hook on the maxillipedal endite.

Of the 18 species of *Synidotea* now known from the eastern Pacific, only *S. francesae* is a regular resident of warm waters (i.e., the Eastern Pacific Zoogeographic Region); all others are temperate or polar species. The genus is worldwide in distribution but notably absent from the New World tropics. Brusca and Wallerstein (1979b) and Wallerstein and Brusca (1982) hypothesized that this absence is due to the inability of *Synidotea* species to develop certain morphological (size; body spination) and life history (early reproduction; predator avoidance behaviors) adaptations that have allowed successful radiation in this region by other genera (e.g., *Erichsonella, Eusymmerus, Parasymmerus*), and that any species of Idoteidae that may be found successfully inhabiting the warm coastal waters of the tropical eastern Pacific would have had to evolve some of these adaptations. In the subtropical waters of the Gulf of California, *S. francesae* has evolved at least 1 (small size) if not more (e.g., early reproduction) of these attributes which presumably have played a role in its ability to survive the predation-intense summers of this region. Menzies and Miller (1972) state that the mean length of the 8 Arctic species of *Synidotea* is 18.8 ± 2.6 mm, while the mean length of the 5 tropical species then known (all from the Old World) was 8.0 ± 2.2 mm. Temperate species fall between these two extremes. By comparison, the largest specimen of *Synidotea francesae* examined is only 6 mm in length.

Genus *Colidotea* Richardson, 1905

The genus *Colidotea* was briefly reviewed by Brusca and Wallerstein (1979b). The genus now contains 4 species: *C. rostrata* (Benedict), southern California; *C. findleyi* Brusca and Wallerstein, Baja California; *C. edmondsoni* Miller, Hawaii; and *C. wallersteini* new species, Baja California (Fig. 7). Brusca (in press) discusses the phylogeny, evolutionary history and zoogeography of *Colidotea* and its sister-group, *Synisoma* Leach. Both genera are restricted to warm-temperate and subtropical waters of the New World (*Colidotea*) and Old World (*Synisoma*). Table 1 summarizes the principal features that distinguish these 2 genera from one another and from all other genera of Idoteinae.

A reexamination of the 4 known species of *Colidotea* warrants an expanded diagnosis of the genus and a key to the species, as follows.

Diagnosis.—Idoteinae with body compact, pereon merging smoothly with pleon. Cephalon with anterolateral angles produced; with or without a medial cephalic process or spine; eyes lateral. Second antennae with flagella comprised of a few, or a dozen or so articles, the number increasing somewhat with age (length). Maxillipedal palp of 4 free articles, apical article large and ovate; epipod present; endite with or without coupling hooks. Mandible with large lacinia mobilis, nearly as large, or as large as incisor process. Pereon with coxal plates present on segments II–VII; coxae may or may not be visible in dorsal aspect, or may be visible only on posteriormost pereonites. Pleon comprised of single piece, with one pair of lateral incisions (=suture lines); pleon length less than ⅓ total body length; uropods uniramous. Appendix masculinum of male arising from base of pleopod 2 endopod. Uropods uniramous.

Key to the Species of *Colidotea*

1. Cephalon with medial spine or process, which may or may not project over supra-antennal line 2
– Cephalon without medial spine or process 3
2. Cephalic process bifurcate (2-pronged); frontal process subacute (convex); pleotelson with posterior margin angulate; bases of pereopods with dark chromatophore band ..... *C. edmondsoni*
– Cephalic process simple (single apex); frontal process notched (concave); pleotelson with posterior margin evenly rounded; bases of pereopods without dark chromatophore band ..... *C. rostrata*
3. Frontal process notched (concave); coxal plates hidden in dorsal aspect; pleotelson posterior margin subacute; eyes large; maxilla 2 trilobate ..... *C. findleyi*
– Frontal process not notched, but convex; coxal plates visible on pereonites IV–VII, in dorsal aspect; pleotelson posterior margin evenly rounded; eyes small; maxilla 2 bilobate ..... *C. wallersteini* new species

Colidotea wallersteini new species
Figures 4, 5

Types.—Holotype: male, AHF 452. Paratypes: AHF 4925; SDNHM (1 specimen); USNM (1 specimen).

Locality.—Known from only two localities. Holotype: México, Baja California Norte (Pacific coast), Punta Clara, south Rio Santo Tomás, 18 December 1945, collected by C. Hubbs (H45–217a). Paratypes: México, Guadalupe Island, off N coast of Baja California, Melpomene Cove, intertidal collections, 18 December 1949, collected by R. J. Menzies and D. Reish, *Velero III* (Allan Hancock Foundation), Station No. 1915-49.

Diagnosis.—Body straight-sided; coxal plates visible in dorsal aspect on pereonites IV–VII. Cephalon with supra-antennal line forming 3 points, 1 medial and 2 submedial; frontal process distally convex; antenna 1 flagellum a single article; antenna 2 flagellum with about 9 articles; lacinia mobili present on both right and left mandible; molar

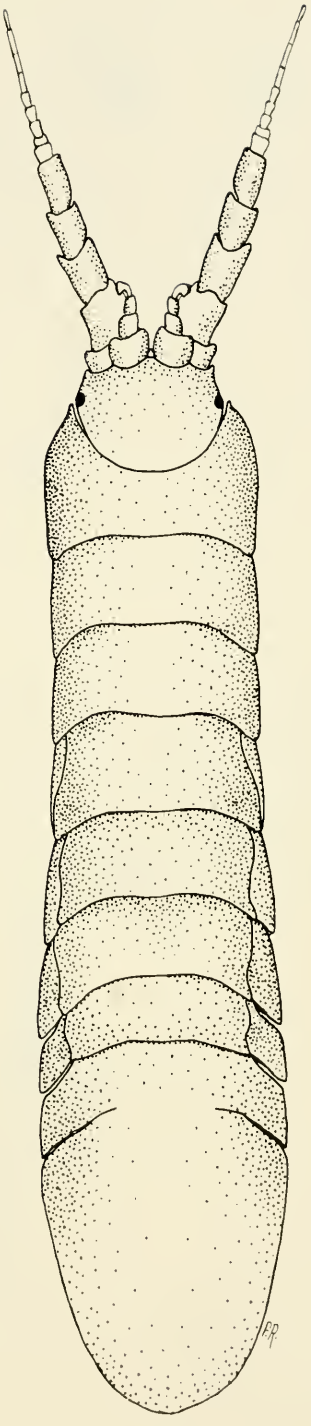

FIGURE 4. *Colidotea wallersteini* new species. Holotype, AHF 452. Male.

process simple, greatly reduced (smaller than lacinia); maxilliped with 2 coupling hooks on right, 1 on left; maxilla 2 bilobate, smaller lobe with 2-jointed apical process terminating in single large seta; posterior margin of pleotelson evenly convex.

Description.—Body smooth, straight-sided, with coxal plates on pereonites II–VII

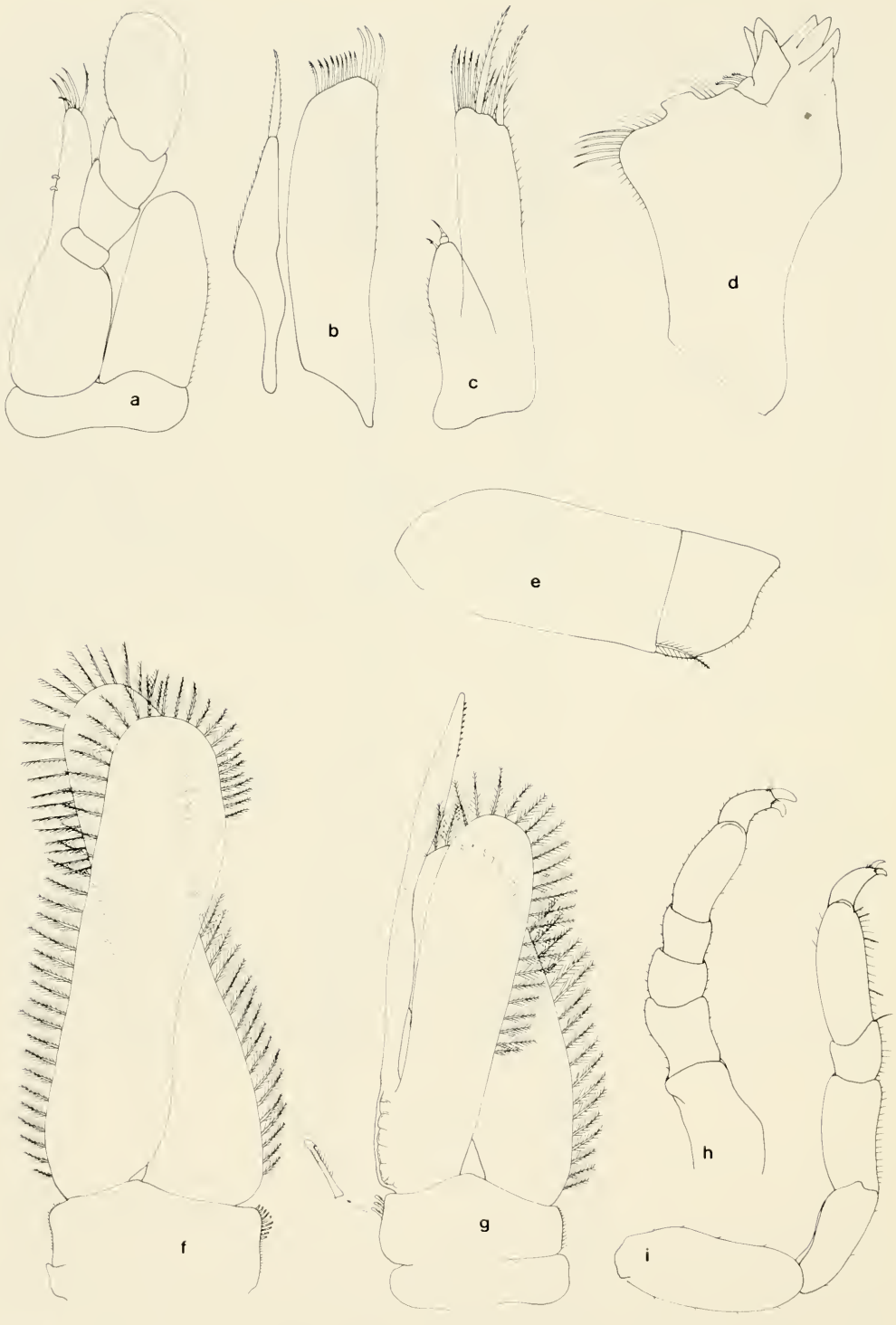

FIGURE 5. *Colidotea wallersteini* new species. Holotype, AHF 452. Male. a, right maxilliped. b, maxilla 1. c, maxilla 2. d, right mandible. e, uropod. f, pleopod 1. g, pleopod 2. h, pereopod IV. i, pereopod I.

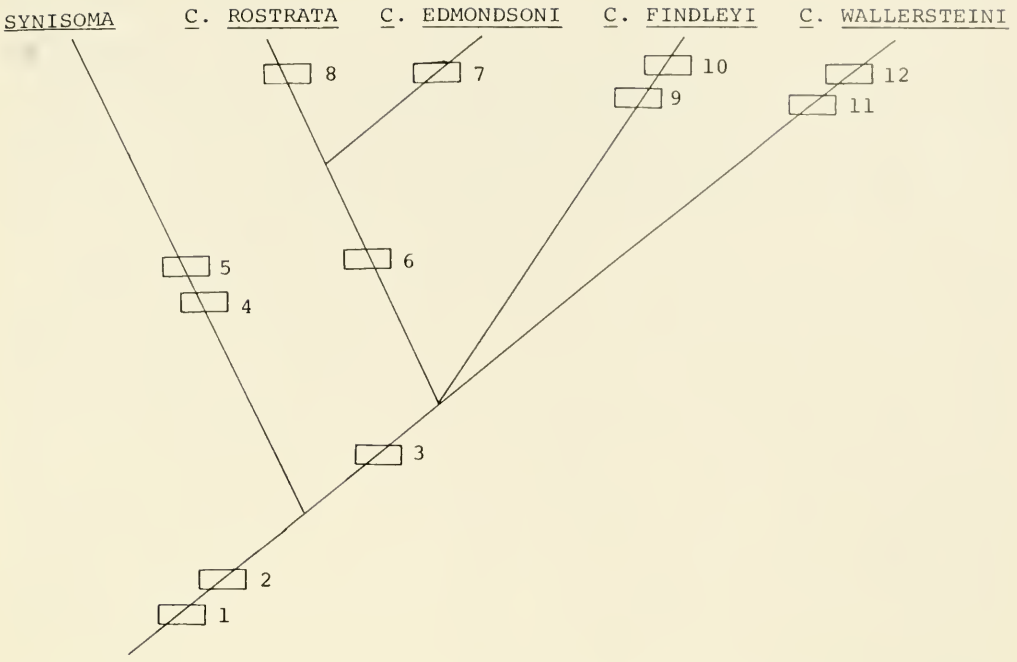

FIGURE 6. Cladistic relationships of the 4 known species of *Colidotea* and their sister-group, *Synisoma*. See Brusca (in press) for character polarity analysis and discussion of relationships outside this clade. Apomorphies indicated are as follow: 1, Reduction from a 5-jointed to a 4-jointed maxillipedal palp. 2, Lacinia mobilis of mandible enlarged, subequal to incisor process. 3, Pleon reduced to a single piece, with a pair of lateral incisions indicating partial fusion of 1 pleomere. 4, Pleon reduced to a single piece, with no remaining lateral incisions. 5, Pleon greatly elongated, ⅓ or more total body length. 6, Cephalon with an anteromedial process. 7, Anteromedial process of cephalon bifid. 8, Adoption of a symbiotic relationship with sea urchins of the genus *Strongylocentrotus*, and associated morphological adaptations (e.g., elliptical body; purple pigmentation). 9, Eyes enlarged. 10, Posterior margin of pleon acute. 11, Second maxillae with only 2 lobes. 12, Typical "spines" of first maxilla outer lobe reduced to 3 slender, stout, simple setae.

(visible in dorsal aspect only on IV–VII). Length to at least 16.5 mm; length 4–5 times width.

Cephalon: Without tubercles or elevations of any kind; broadly immersed in pereonite I; frontal process distally convex. Eyes very small, set on extreme lateral margins. Antenna 1 comprised of 4 articles, fourth being the single flagellar article, with terminal esthetascs. Antenna 2 with 9-articulate flagellum. Mandible with 4-toothed incisor; lacinia with 3 teeth and 3 stout setae; molar process greatly reduced, simple. Maxilla 1 outer lobe with about 9 small apical setae (some of which are comb setae) and 3 stout simple setae; inner lobe ending in single stout setose spine. Maxilla 2 bilobate; larger lobe with 2 very large plumose setae and about 7 smaller setae, some ctenose; smaller lobe with 2-jointed apical process terminating in single large seta. Maxilliped typical for genus; endite with several large apical setae; 2 coupling hooks on right, 1 on left.

Pereon: Smooth, straight-sided, forming continuous line with pleon; pereonite I with anterolateral angles produced to level of eyes, engulfing cephalon. Pereonites gradually increasing in width posteriorly; II–VI subequal in length; I and VII somewhat shorter than others. Well-developed coxal plates present on II–VII, visible in dorsal aspect only on IV–VII. Pereopods I–VII slender and ambulatory, terminating in reflexed, biungulate dactyl; setation simple; ischium of pereopod I grooved to receive basis.

Pleon: Posterior margin of pleotelson evenly convex. Uropods simple; with single large plumose seta at junction of protopod and lamella. Pleopods typical of genus; 1–2 with abundant plumose marginal setae; 3–5 reduced, somewhat fleshy, and either

FIGURE 7. Distributions (locality records) of the known species of *Colidotea*. Open circle = *C. wallersteini*. Closed circle = *C. findleyi*. Triangles = *C. rostrata*. *C. edmondsoni* is endemic to the Hawaiian Islands (not on map).

naked or at most with a few scattered simple setae (as in *C. findleyi*). Appendix masculina large, extended beyond apex of pleopodal lamellae, with short apical spines; base of pleopod 2 endopod "muscularized" just below junction of appendix maxulinum.

Etymology.—*Colidotea wallersteini* is named in honor of Dr. Barry Wallerstein, in acknowledgment of his work on the systematics and ecology of the Idoteidae and

in recognition of his long-standing friendship; furthermore, the resemblance in form is striking.

Discussion.—Of the 4 known species of *Colidotea*, 2 (*C. rostrata* and *C. edmondsoni*) share a unique derived character, the large cephalic tubercle. In addition to this synapomorphy, they have more general characters in common with one another than either shares with *C. findleyi* or *C. wallersteini*. No synapomorphies are recognizable to unite the latter 2 taxa as sister-species, so their cladistic relationship must be viewed as a trichotomy at this time. The character relationships of the known species of *Colidotea* are expressed in the cladogram in Fig. 6.

Because Hawaii arose as an oceanic island, *C. edmondsoni* most likely evolved there in isolation subsequent to a dispersal event from western North America. Its immediate ancestor was probably a free-living species that was also the parent taxon to the commensal *C. rostrata*. *Colidotea findleyi* and *C. wallersteini* can be derived from this same ancestral lineage. The latter is strictly a warm-temperate species, known only from northwestern Baja California and Guadalupe Island (Fig. 7). *Colidotea findleyi* is also a warm-temperate species, but exhibits considerable eurythermy in its ability to survive the warm summer months typical of the northern Gulf of California. The disjunct occurrence of *C. findleyi* on both the western coast of Baja California (and Guadalupe Island), as well as the restricted northern Gulf of California population, suggests that it may have entered the Gulf during a period of lowered oceanic paleoisotherms (i.e., Pleistocene glacial periods). Brusca and Wallerstein (1979b) and Wallerstein and Brusca (1982) have discussed the probability of such events, suggesting that the Pleistocene glacials and interglacials (and the associated latitudinal shifts in coastal isotherms) resulted in a series of vicariant events such that populations of temperate species were repeatedly trapped in the northern Gulf of California as latitudinal isotherms shifted from north to south and back. These events were probably responsible for the evolution of the various northern Gulf endemic species that have warm-temperate (Californian) sister-taxa. If this theory is correct, *C. findleyi* can most simply be envisioned as a sister-species of *C. wallersteini*, the 2 taxa being vicariant products of one of the earlier Pleistocene glacial episodes. Sympatry was later effected when a subsequent glacial event facilitated the escape of *C. findleyi* from the Gulf. The present interglacial period and relatively high coastal isotherms maintain the current disjunct distribution of *C. findleyi*.

Acknowledgments

This study was funded by a grant from the National Science Foundation (DEB 80-17835). Appreciation is extended to Bill Cooke, George Schultz, and Tom Bowman for the loan of specimens of *Colidotea edmondsoni*; to the British Museum (Natural History) for the loan of *Synisoma* specimens; and to Fred Schram and Greg Pregill for reviewing the manuscript. Frances Runyan executed the two dorsal views.

Literature Cited

Brusca, R. C. In press. Phylogeny, evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Idoteidae). San Diego Soc. Nat. Hist. Trans.

———, and B. R. Wallerstein. 1979a. The marine isopod crustaceans of the Gulf of California. II. Idoteidae. New genus, new species, new records and comments on the morphology, taxonomy and evolution within the family. Proc. Biol. Soc. Wash. 92(2):253–271.

———. 1979b. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow-water zoogeography for the region. Bull. Biol. Soc. Wash. 3:67–105.

Iverson, E. W. 1972. A new subtidal *Synidotea* from central California (Crustacea: Isopoda). Proc. Biol. Soc. Wash. 85(47):541–548.

Menzies, R. J. 1950. The taxonomy, ecology and distribution of northern California isopods of the genus *Idothea* with the description of a new species. Wasmann J. Biol. 8(2):155–195.

———, and M. A. Miller. 1972. Systematics and zoogeography of the genus *Synidotea* (Crustacea: Isopoda) with an account of Californian species. Smithson. Contrib. Zool., No. 102:1–33.

Wallerstein, B. R., and R. C. Brusca. 1982. Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow-water idoteid isopods (Crustacea: Isopoda: Idoteidae). J. Biogeogr. 9:135–150.

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Descriptions of five new muricacean gastropods and comments on two additional species, in the Families Muricidae and Coralliophilidae: (Mollusca)

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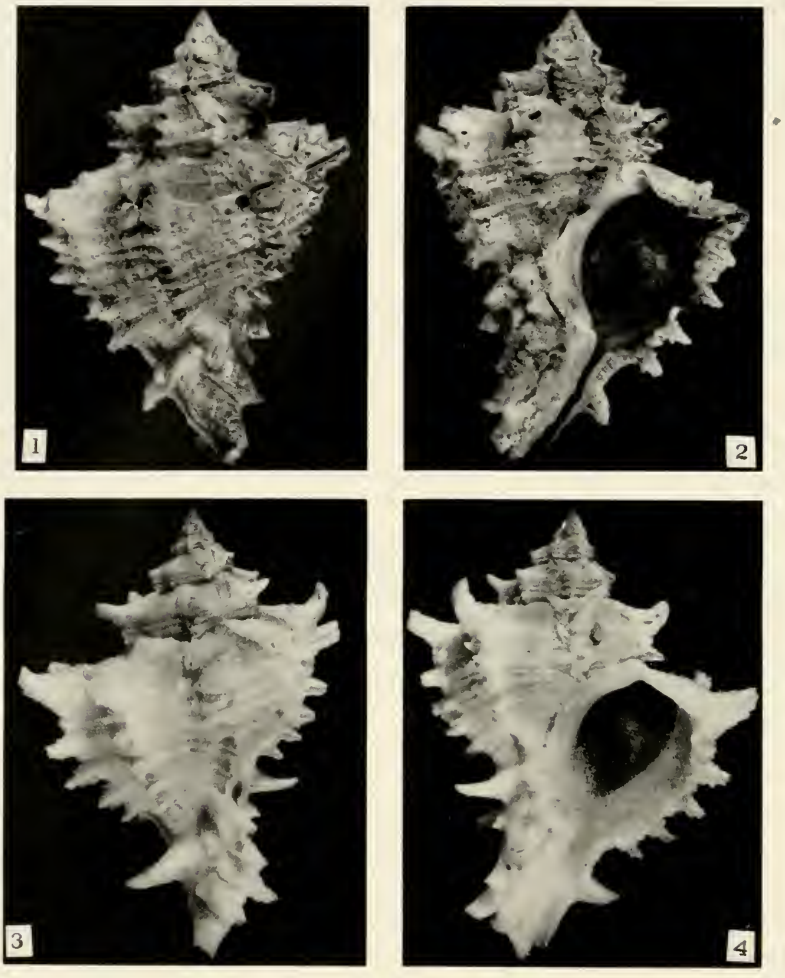
Abstract. Five new species of muricacean (superfamily Muricacea) gastropods, one muricid and four coralliophilids, are described as follows: from the Persian Gulf, *Hexaplex rileyi* (Muricidae: Muricinae); from Isla Isabella (=Albemarle Island), Galápagos Islands, *Babelomurex deroyorum* (Coralliophilidae); from Cebu Island, Philippine Islands, *Babelomurex jeanneae, Coralliophila armeniaca* and *Coralliophila caroleae* (Coralliophilidae). Additional comments and illustrations are provided on protoconch and opercular characters of *Coralliophila neritoidea* (Lamarck 1816), the type of *Coralliophila*, and for *Coralliophila erosa* (Röding 1798). The latter two species occur intertidally and subtidally on coral reefs in the tropical Indo-Pacific Ocean.

Introduction

Within the Muricidae, the genus *Hexaplex* Perry, 1811, includes those species with a solid and globose shell bearing five to eight spinose more or less foliaceus varices. The type species, *Hexaplex cichoreum* (Gmelin 1791) occurs in the Philippine Islands. Specimens from the Persian Gulf, heretofore unknown, are referable to this genus as a new species, which we describe in this report. We compare this new taxa to related species from the Mediterranean Sea, Indian Ocean and western Atlantic Ocean.

Four new species of Coralliophilidae are also described here. The Coralliophilidae is separable from all other muricacean families in lacking a radula (Thiele 1929, Robertson 1970). The members of this family feed suctorially and most are recognized as ectoparasites or predators on various species of Cnidaria. These mollusks move from host to host, though they are not known to be highly destructive to their prey (Ward 1965, Robertson 1970, 1980). They have a thaid type operculum with a lateral nucleus. Unfortunately shell characters for this family are unstable taxonomic criteria and the relationships within the family are complicated further by the lack of a radula. The radula is often a distinctive character in the classification of other muricacean taxa at the generic level. Twenty-seven genera of Coralliophilidae were enumerated by D'Attilio (1978) and four more have since been added (D'Attilio 1979, Kosuge 1979), bringing the total to 31. The two genera considered herein are *Coralliophila* H. and A. Adams, 1853, and *Babelomurex* Coen, 1922. In *Coralliophila* a spinose spiral keel is wanting and there is little sign of episodic growth. Rather growth takes place in continuous increments. Species assigned to *Babelomurex* possess a spinose shoulder keel and may have additional spinose keels on the body whorl. The leading edge of the spines usually indicates growth in an episodic manner similar to varices in the Muricidae.

In addition to the five new species, two others are discussed: *Coralliophila erosa* (Röding 1798) and *C. neritoidea* (Lamarck 1816). These two species are widespread in the Indo-Pacific, where they inhabit intertidal and subtidal coral reefs. Illustrations of certain morphological details for these two species have not been published previously.



FIGURES 1–4. *Hexaplex rileyi* D'Attilio & Myers. Dorsal (1) and apertural (2) views of holotype, SDNHM 81618. Dorsal (3) and apertural (4) views of paratype, SDNHM 81617a.

The following abbreviations are used: SDNHM (San Diego Natural History Museum); AMNH (American Museum of Natural History, New York); and USNM (National Museum of Natural History, Washington, D.C.).

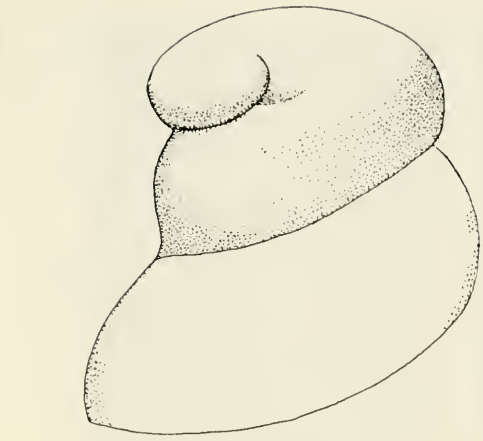
SYSTEMATIC ACCOUNT

Phylum Mollusca
Superfamily Muricacea
Family Muricidae Rafinesque, 1815
Subfamily Muricinae Rafinesque, 1815
Genus *Hexaplex* Perry, 1811

Type species.—*Hexaplex foliacea* Perry, 1811 by subsequent designation Iredale 1915 (=*Murex cichoreum* Gmelin, 1791).

Hexaplex rileyi new species
Figures 1–6

[Note: Biggs (1973:pl. 5, figs. 8, 9) figured a specimen of *Hexaplex rileyi*, but erroneously referred it to *Murex küsterianus* (Tapparone-Canefri 1875).]



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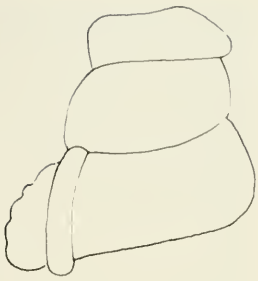

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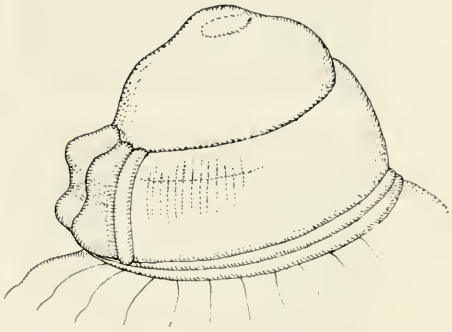

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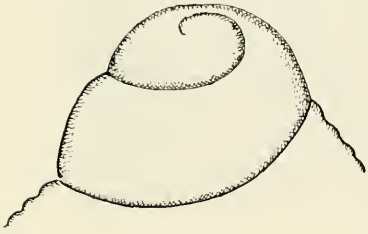

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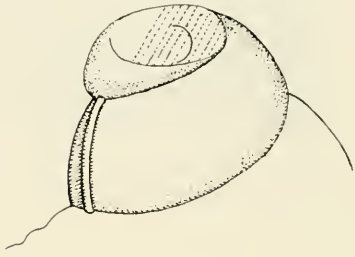

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FIGURES 5 AND 6. Detail drawing of the protoconch of *Hexaplex rileyi* from SDNHM 81617b.
FIGURES 7 AND 8. Detail drawing of the protoconch of *Hexaplex fulvescens* (Sowerby 1834). SDNHM 81620.
FIGURE 9. Detail drawing of the protoconch of *Hexaplex küsterianus* (Tapparone-Canefri 1875). SDNHM 78106.

Description.—Shell broadly biconic; grayish white with three pale brown bands distributed evenly over body whorl, bands mostly distinguishable within outer aperture. Protoconch of holotype eroded. Six weakly sloping, tabulate postnuclear whorls; suture impressed. Aperture ovate, comparatively large; outer lip crenulate, reflecting external sculpture; inner lip white, mostly appressed; anal sulcus well-defined, U-shaped. Siphonal canal open, of moderate length, bent to left and recurved, with five previous canal terminations; umbilical chink present. Axial sculpture of nine strong, spinose varices on body whorl which cross shoulder and terminate at suture. Five lamellose major cords terminate in open spines on each varix; between major cords are numerous minor cords of varying width. Entire shell including shoulder finely scabrous. A prominent single row of open spines on siphonal canal with space separating this row of spines from those on body whorl.

Color.—Grayish white with three weak brown bands.

Type material.—Holotype: SDNHM 81618. Paratypes: SDNHM 81617a and 81617b; AMNH 213801; USNM 819632.

Other material examined.—Twelve specimens from the type locality, Kenneth Riley collection.

Type locality.—64 km offshore, United Arab Emirates in The Gulf (Persian); depth 15 m; clinging to petroleum field rigs.

Dimensions (in mm).—

		Length	Width
SDNHM 81618 (holotype)		51.0	36.8
SDNHM 81617a (paratype)		47.0	36.5
SDNHM 81617b (paratype)		21.0	15.8
USNM 819632 (paratype)		39.0	29.5
AMNH 213801 (paratype)		33.0	25.0
12 uncatalogued specimens	from	26.5	19.5
in the K. Riley coll.	to	43.9	31.4

Etymology.—Named for Mr. Kenneth Riley, a petroleum engineer who collected the specimens.

Discussion.—The color of this species ranges from pure white to pale brownish white with indistinct brown bands. The varices number from six to nine and the postnuclear whorls from five to six. Protoconch of paratype SDNHM 81617b has two and one-third smooth whorls, somewhat tabulate and of nearly equal diameter.

This new species is similar to *Hexaplex trunculus* (Linné 1758) from the Mediterranean Sea. *Hexaplex trunculus,* however, has a higher spire, is less tabulate, the body whorl is more convex and bulges at the shoulder, and the aperture is larger.

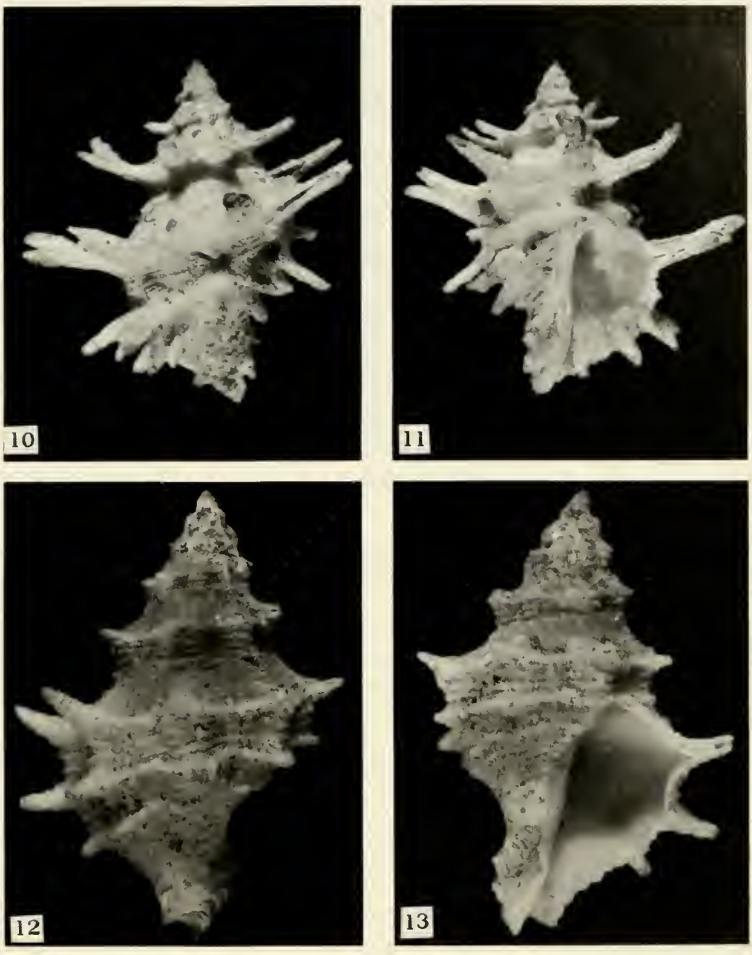
Further comparison can be made with *Hexaplex fulvescens* (Sowerby 1834), which occurs in the western Atlantic and the Gulf of Mexico, and *H. küsterianus* (Tapparone-Canefri 1875) from the Indian Ocean. *Hexaplex fulvescens* has a much larger shell (to 200 mm), the shoulder is non-tabulate, suture weakly impressed, aperture denticulate, and canal much longer. In addition, the varices are concave on their receding side, and the shell is white with reddish brown lines over the spiral threads of the entire shell. *Hexaplex fulvescens* has a protoconch of three convex whorls which show very weak axial grooves (Figs. 7, 8). *Hexaplex küsterianus* has a broad shell with a low spire and indistinct suture. The body whorl is very broad and the aperture large. The protoconch of *H. küsterianus* has an indistinct number of convex whorls (Fig. 9).

Family Coralliophilidae Chenu, 1859
Genus *Babelomurex* Coen, 1922

Type species.—*Fusus babelis* Requien, 1848 by original designation.

Babelomurex deroyorum new species
Figures 10–14

Description.—Shell broadly fusiform; spire moderately high; suture weakly impressed. Protoconch of holotype eroded; teleoconch of six whorls; aperture large, ovate; outer lip sharp, with spiral grooves resulting from open spines at margin. Anal sulcus broad, shallow; inner lip demarked by elongate node; canal short, open, recurved; siphonal fasciole with chink and five short canal terminations. Axial sculpture of ten varices with weakly defined margins on body whorl; penultimate body whorl with nine varices; strong shoulder keel separated by gap from two close-set keels below. Narrow, flatly triangular, relatively long spines arise at varical margins; spines on keel directly below shorter, and those on most anterior keel progressively shorter; presence of terminal portions of secondary keel obscuring suture; fine squamous threads covering entire surface, including upper and lower surface of spines; spiral threads coarser on canal.



FIGURES 10–13. *Babelomurex deroyorum* D'Attilio & Myers. Dorsal (10) and apertural (11) views of holotype, SDNHM 81613. Dorsal (12) and apertural (13) views of paratype, SDNHM 81616a.

Color.—White, showing some slight attrition; small patches are covered with a red hydrocoral or bryozoan; paratypes with a lustrous white aperture.

Type material.—Holotype: SDNHM 81613. Paratypes: SDNHM 81616a, 81616b, and 81616c; USNM 819633a and 819633b; AMNH 213802a and 213802b.

Type locality.—Dredged from 75–100 m off Isla Isabella (Albemarle Island), Tagus Cove, Galápagos Islands; January 1969.

Dimensions (in mm).—

	Length	Width
SDNHM 81613 (holotype)	28.8	29.3
SDNHM 81616a (paratype)	17.0	12.5
SDNHM 81616b (paratype)	12.2	8.9
SDNHM 81616c (paratype)	8.4	7.4
AMNH 213802a (paratype)	13.8	11.0
AMNH 213802b (paratype)	9.8	9.2
USNM 819633a (paratype)	12.7	9.0
USNM 819633b (paratype)	8.0	5.5

Etymology.—Named for the collectors, Mr. and Mrs. Andre DeRoy, who through their collecting efforts, have contributed to our understanding of the endemic molluscan fauna of the Galápagos Islands.

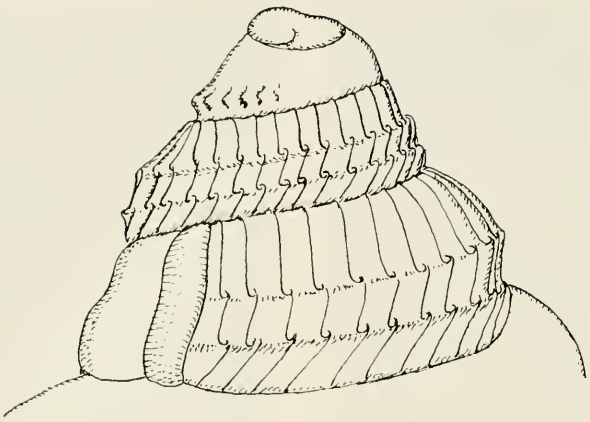


FIGURE 14. Detail drawing of the protoconch of *Babelomurex deroyorum* from SDNHM 81616c.

Discussion.—In addition to the holotype, which is a dead empty shell showing some attrition, seven smaller specimens were studied, the largest of which possesses five whorls. The keel, showing spines, appears clearly on the third postnuclear whorl. Protoconch of SDNHM 81616c has three and one-half whorls with a spiral cord in the center and a second spiral cord below; axial threads are diagonal to the protoconch, knob-like across the spiral cords. This new species differs from all other eastern Pacific and western Atlantic species in the narrow, elongate spines, and finer squamous sculpture. This species was recovered from the same area as *Babelomurex santacruzensis* (Emerson and D'Attilio 1970) which has a single row of spines on the shoulder and is more closely related to *B. dalli* (Emerson and D'Attilio 1963) from the western Atlantic. Other eastern Pacific species are *B. oldroydi* (Oldroyd 1929), *B. costata* (Blainville 1832), and *B. hindsi* (Carpenter 1857). *Babelomurex oldroydi* is found off the California coast and has a larger, heavier, coarser shell than *B. deroyorum* and possesses three spinose keels. *Babelomurex costata* is similar to *B. oldroydi,* but with less developed and variably keeled spiny cords; *B. hindsi* is smaller than any of these species.

Babelomurex jeanneae new species
Figures 15–20

Description.—Shell biconically fusiform; height from top of aperture to canal termination, 10 mm. Protoconch of holotype eroded; six postnuclear angulate whorls with large spinose keel at shoulder angle; suture obscured by anteriorly directed, scabrous-edged spinose keel corresponding to secondary keel on body whorl; aperture relatively large, ovate; columella pillar straight except for slight concavity midway; inner lip edge weakly erect anteriorly, outer lip (not entirely mature) extending into the open spines; siphonal canal short, broad, open, recurved; fasciole strongly sculptured, with four older canal terminations; umbilical chink narrow but deep; seven varices on body whorl, eight on penultimate whorl; all varices terminating in lengthy spines. Spiral sculpture of a primary row of broad, contiguous, open spines forming the keel; growth of spines episodic, giving them a scaly or foliated appearance. Outer portion of primary spine bent in direction of growth and entire spiny keel recurved posteriorly; second and third row of spines below; bases of secondary spines contiguous and forming keels. Five progressively smaller scabrous rows of spines on canal; one similar scaly row between second and third row of spines; six rows of weak scabrous spiral cords above shoulder terminating at apertural margin.

FIGURES 15 AND 16. *Babelomurex jeanneae* D'Attilio & Myers. Dorsal (15) and apertural (16) views of holotype, SDNHM 79499.

Color.—Creamy white, stained with pale ochre in depressed part of shoulder and body at receding side of margin.

Type material.—Holotype: SDNHM 79499. Paratypes: SDNHM 79500 and 81402.

Other material examined.—One specimen in the Rose D'Attilio collection, one specimen in the Barbara W. Myers collection and one specimen in the Donald Pisor collection.

Type locality.—Bohol Straits between the Islands of Cebu and Bohol in the Philippine Islands.

Dimensions (in mm).—

	Length	Width
SDNHM 79499 (holotype)	21.5	25.5
SDNHM 81402 (paratype)	22.9	25.9
SDNHM 79500 (paratype)	23.5	22.0
R. D'Attilio coll.	17.0	29.0
B. W. Myers coll.	23.0	25.0
D. Pisor coll.	22.0	24.5

Etymology.—Named for Jeanne Pisor, who with her husband Donald Pisor, have made noteworthy contributions to the molluscan collections of the San Diego Natural History Museum.

Discussion.—There may be one or two spiny cords below the shoulder keel; the number of cords below the secondary keel varies from four to six; growth striae may be strong. SDNHM 79500, with a mature outer lip, retains a white intritacalx, a chalky white surface layer in some mollusks (D'Attilio and Radwin 1971), with no color other than the white surface. The specimen in the R. D'Attilio collection has unusually broad, lengthy spines. The protoconch on this specimen has two and one-half whorls; the earliest portion is smooth, followed by a sculptured portion with five close-set axial striae and two spiral cords, beaded where crossed by striae. The specimen in the Barbara W. Myers collection is white flushed with a pale violet-pink, and the spines curve strongly in the direction of growth.

Babelomurex jeanneae probably belongs to a complex of species, the best known of which is *B. pagodus* [of authors, not *B. pagodus* (A. Adams 1853) (see D'Attilio 1983)]. Characters similar to *B. pagodus* are the possession of a spinose keel at the shoulder and a secondary keel midway on the body whorl followed anteriorly by a

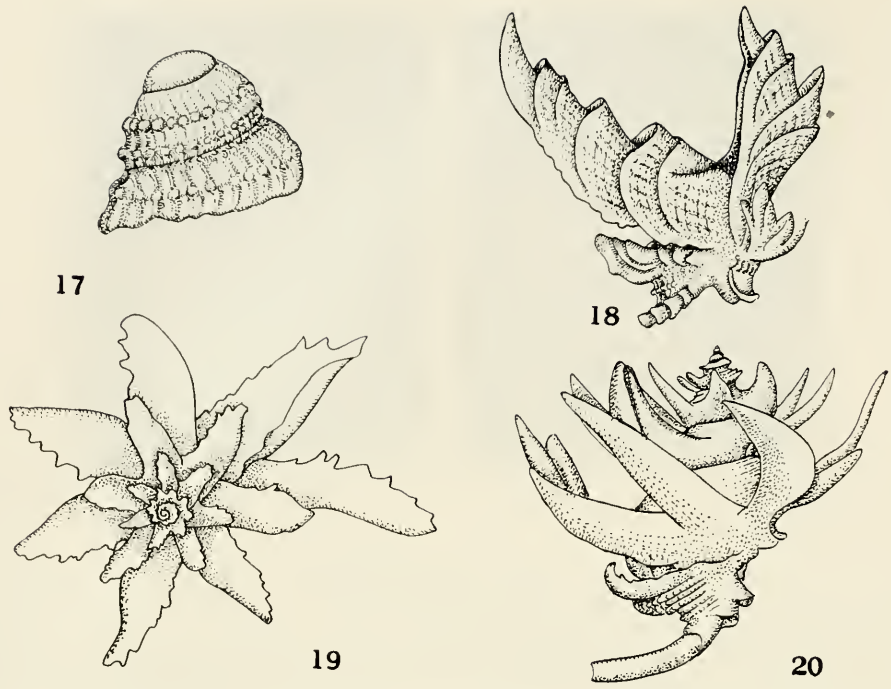
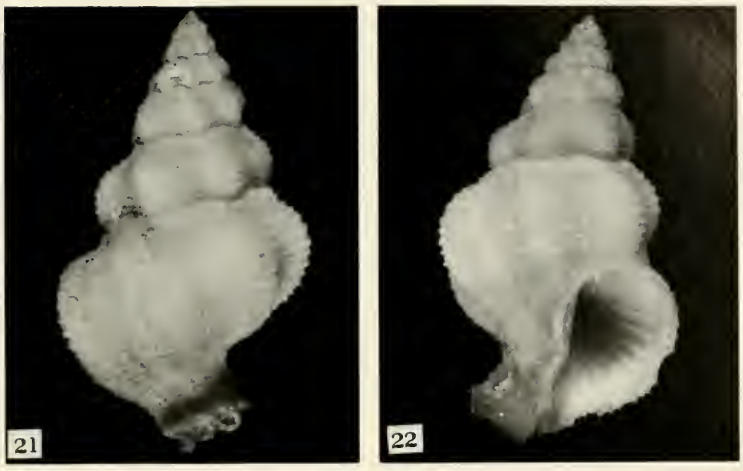


FIGURE 17. Detail drawing of the protoconch of *Babelomurex jeanneae* from specimen in the Rose D'Attilio collection.
FIGURES 18 AND 19. *Babelomurex jeanneae.* Specimen from the Rose D'Attilio collection. Detail of spine formation showing scales or foliations (18). Detail of broad spines as viewed from above (19).
FIGURE 20. *Babelomurex jeanneae.* Detail showing spines curved in the direction of growth from specimen in the B. W. Myers collection.

series of progressively diminishing spinose cords. *Babelomurex pagodus* also has a white shell shaded with ochre in the concave portions of the intervarical areas. Varical spinose projections also number around eight and are sharply triangulate. *Babelomurex pagodus* is well known and common in southeastern Japan. Based on literature records its geographic range is extensive, being known throughout the central and western Pacific. As far as is known from the extensive collecting done in Japan, *B. jeanneae* does not occur there. Cebu specimens of *B. pagodus* resemble in shell morphology specimens from southeastern Japan.

Babelomurex fruiticosus (Kosuge 1979), described from specimens obtained in the Straits of Bohol between Cebu and Bohol Islands, has some similarity to *B. jeanneae* in its possession of a spinose keel at the shoulder and one midway on the body whorl. However, the spire is comparatively higher, the area below the shoulder keel shorter, appearing compressed, and there are only two spinose cords. The spines are narrow, often very elongate, bent or recurved, and their receding side ornamented with sharply pointed narrow spinelets imparting to the spines a resemblance to deer antlers. In addition, the entire shell is suffused with rich pink or pink-violet, or at times creamy white with red-brown at the keel concentrated on the receding side of the varix.

Babelomurex cristatis (Kosuge 1979) also has conchological characters similar to *B. jeanneae.* However, the eight shoulder keel spines in *B. cristatus* are shorter, strongly up-turned and recurved, with spinelets on their receding side; the secondary keel on the mid-area of the body whorl is mostly non-spinose except in mature specimens. Two or three inconspicuous cords occur below the mid-cord, and a nearly obsolete spiral cord may be present on the canal; the intervarical areas are relatively broad and the shell surface is finely and scabrously striate; the color is light to dark tan (flesh), occasionally being a deeper brown in the concave areas between the strongly formed, rounded, axial costae.



FIGURES 21 AND 22. *Coralliophila armeniaca* D'Attilio & Myers. Dorsal (21) and apertural (22) views of holotype, SDNHM 79507.

Genus *Coralliophila* H. and A. Adams, 1853

Type species by subsequent designation Iredale 1912: "*Murex neritoideus* Chem. [nitz]" = *Murex neritoideus* Gmelin, 1791, not Linné, 1767 = *Fusus neritoideus* Lamarck, 1816 (syn. *Purpura violacea* and *P. diversiformis* Kiener, 1836).

Coralliophila armeniaca new species
Figures 21–24

Description.—Shell fusiform above, compressed anteriorly. Protoconch of holotype eroded; six postnuclear convex whorls; suture wavy, distinct; body whorl large, sharply

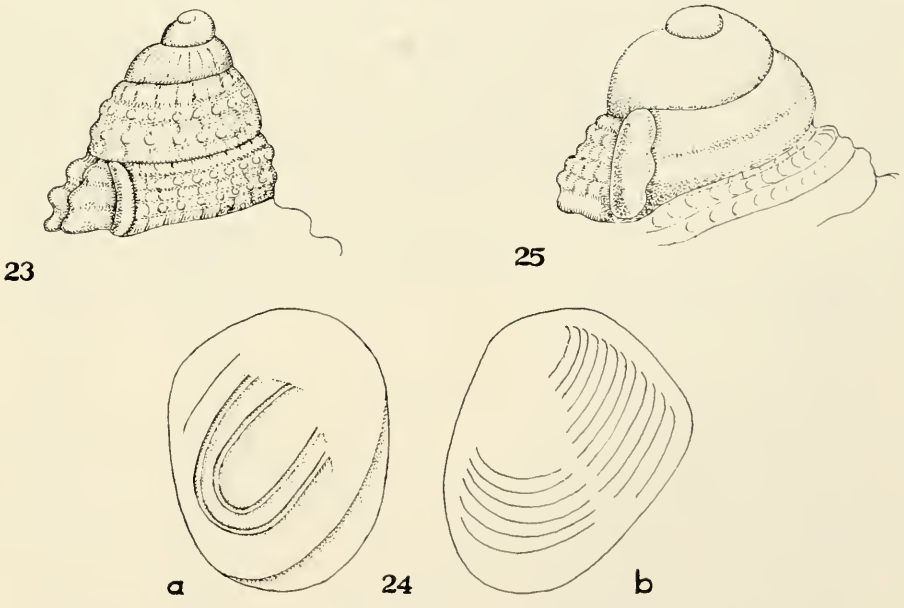


FIGURE 23. Detail drawing of the protoconch of *Coralliophila armeniaca* from SDNHM 79504i.
FIGURE 24 (a) AND (b). Detail drawing of the operculum of *Coralliophila armeniaca* from holotype, SDNHM 79507. Internal (a) and external (b) views.
FIGURE 25. Detail drawing of the protoconch of *Coralliophila rosacea* (Smith 1903) from SDNHM 72131.

FIGURES 26 AND 27. *Coralliophila caroleae* D'Attilio & Myers. Dorsal (26) and apertural (27) views of holotype, SDNHM 79505.

incurved below, flaring out at siphonal fasciole. Aperture large with ten lengthy lirae within; lirae at the crenulate outer lip more numerous, reflecting external spiral sculpture; inner lip erect on lower two-thirds, adherent above. Anal sulcus very weak posteriorly at juncture of outer lip and columella; siphonal canal open, relatively short and broad, recurved, with numerous strong canal terminations on the flaring fasciole, umbilical chink present. Shell with axial sculpture of six swollen, rounded ribs set close together, terminating at base of body whorl below and diminishing in strength as they abut the whorl above. Spiral sculpture of primary and secondary cords form entire surface of the shell; about 15 primary cords with intercalary secondary cords on the body whorl below the shoulder; similar cords covering the shoulder; all cords weak to strongly scabrous. Operculum thin, translucent, amber-brown with concentric ridges externally; internally with two small cords; horseshoe shaped.

Color.—Deep apricot with slight orange cast; paratypes range from violet to apricot-pink. Aperture pale orange at edge of outer lip, white within and on the columella.

Type material.—Holotype: SDNHM 79507. Paratypes: SDNHM 79504a–j; USNM 819634a and 819634b; AMNH 213803a and 213803b.

Type locality.—All specimens from approximately 75 m depth off Cebu Island, in the Bohol Straits, Philippine Islands; obtained with ground nets.

Dimensions (in mm).—

	Length	Width
SDNHM 79507 (holotype)	20.5	11.9
SDNHM 79504a (paratype)	20.0	10.2
SDNHM 79504b (paratype)	18.5	10.5
SDNHM 79504c (paratype)	17.2	8.9
SDNHM 79504d (paratype)	12.5	6.4
SDNHM 79504e (paratype)	13.9	7.3
SDNHM 79504f (paratype)	12.8	6.8
SDNHM 79504g (paratype)	12.1	6.2
SDNHM 79504h (paratype)	10.0	5.0
SDNHM 79504i (paratype)	9.0	5.0
SDNHM 79504j (paratype)	9.8	5.0
AMNH 213803a (paratype)	13.5	7.0
AMNH 213803b (paratype)	8.0	4.5
USNM 819634a (paratype)	15.0	8.0
USNM 819634b (paratype)	7.0	4.0

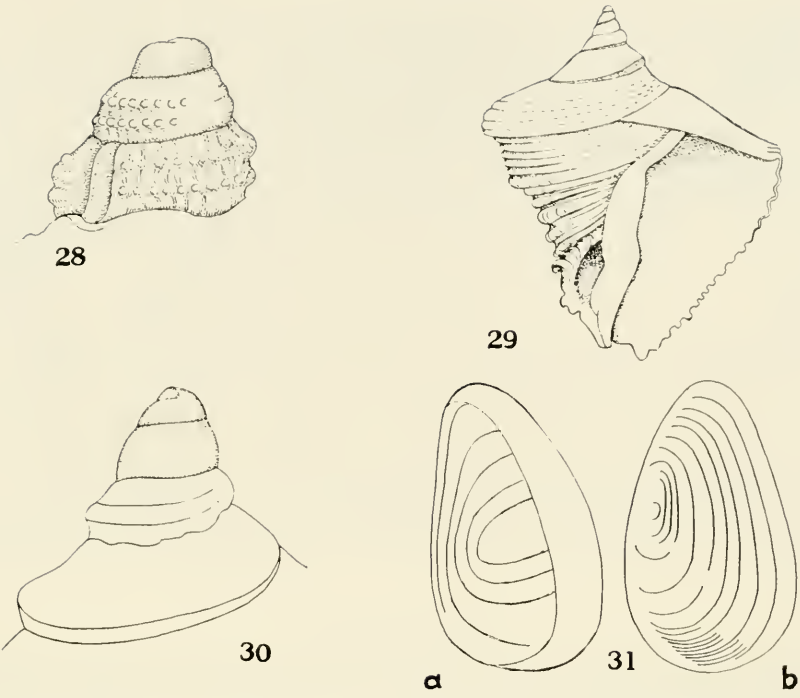


FIGURE 28. Detail drawing of the protoconch of *Coralliophila caroleae* from holotype, SDNHM 79505.
FIGURE 29. *Coralliophila neritoidea* (Lamarck 1816). Apertural view of a juvenile SDNHM 66538.
FIGURE 30. Detail drawing of protoconch of *C. neritoidea* from SDNHM 66538.
FIGURE 31 (a) AND (b). Detail drawing of operculum of *C. neritoidea* from SDNHM 66538. Internal (a) and external (b) views.

Etymology.—From *armeniacus*, referring to the color of ripe apricot fruit.

Discussion.—This species appears closely allied to *Coralliophila fritschi* (von Martens 1874) and *C. rosacea* (Smith 1903), both from South Africa. Another apparently closely related species is *C. arbutum* (Woolacott 1954) (=*Rhombothais arbutum* Woolacott 1954) from New South Wales, Australia. These three species differ from *C. armeniaca* by their possession of broadly fusiform shells with a larger body whorl, widest at mid-height. In contrast, *C. armeniaca* has a relatively high spire and the shell is broadest well below mid-height. In addition, the angulate shoulder of *C. arbutum* gives it a biconic shape. Protoconch of SDNHM 79504i has three and one-half whorls: the first whorl is smooth and rounded whereas the remaining whorls have two spiral cords crossed by axial ridges and the nodes are poorly developed where the axial and spiral sculpture cross. The protoconch of *C. rosacea* is illustrated for comparison (Fig. 25).

Coralliophila caroleae new species
Figures 26–28

Description.—Shell small, biconic; spire concave, low to moderate height; body whorl swollen with moderately angled shoulder tapering to a short, open canal. Protoconch of nearly three whorls, ridged and beaded. Six postnuclear whorls, moderately angled; suture not clear as each succeeding whorl encroaches and somewhat submerges previous whorl up to body whorl where suture is clearly defined. Aperture wide, with sinuous crenulate outer lip; inner lip smooth, adherent posteriorly; canal short and open. Siphonal fasciole composed of a curving scabrous ridge; umbilical chink moderately deep. Axial sculpture beginning on first postnuclear whorl with nine ribs, increasing to 14 on subsequent whorls and fading at fourth postnuclear whorl, becoming

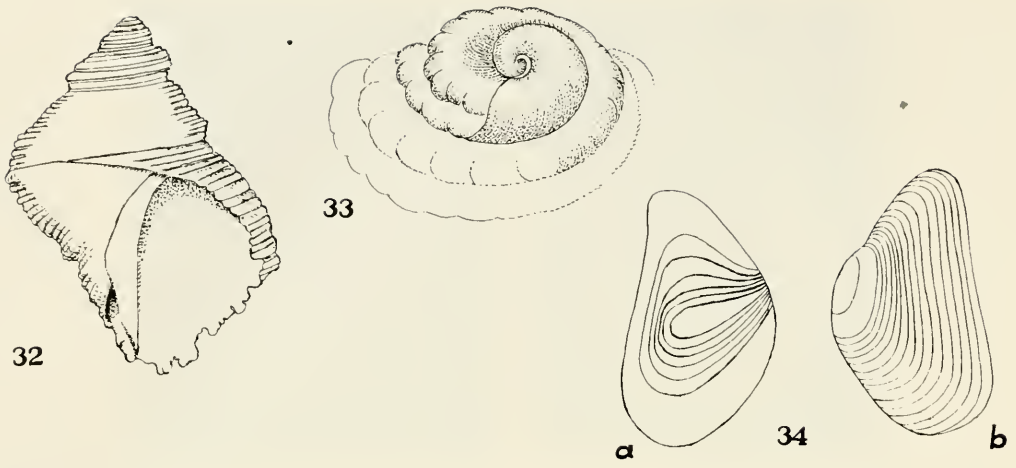


FIGURE 32. *Coralliophila erosa* (Röding 1798). Apertural view of a juvenile SDNHM 77174.
FIGURE 33. Detail drawing of the protoconch of *Coralliophila erosa* from SDNHM 77174.
FIGURE 34 (a) AND (b). Detail drawing of the operculum of *C. erosa* from SDNHM 77174. Internal (a) and external (b) views.

barely visible on body whorl. Spiral sculpture of scabrous major and minor cords above and below periphery, with strong major cord at periphery of each whorl. Body whorl with 11 cords between suture and periphery, and 28 cords from periphery to canal; width of cords variable; interspaces narrow.

Color.—Dull orange; aperture orange; inner lip pale orange.

Type material.—Holotype: SDNHM 79505. Paratypes: SDNHM 79503 and 81614.

Other material examined.—One specimen in the Donald Pisor collection and one specimen in the James Springsteen collection.

Type locality.—Bohol Straits between the Islands of Cebu and Bohol in the Philippine Islands, dredged with bottom nets at 75–100 m.

Dimensions (in mm).—

	Length	Width
SDNHM 79505 (holotype)	19.2	13.6
SDNHM 79503 (paratype)	14.3	11.0
SDNHM 81614 (paratype)	16.8	9.2
D. Pisor coll.	15.1	11.8
J. Springsteen coll.	12.5	7.9

Etymology.—Named for friend and co-worker, Carole M. Hertz.

Discussion.—This new species is similar to two other deep water species from Mactan Island, Cebu, Philippine Islands: *Coralliophila elvirae* D'Attilio and Emerson, 1980, and *C. solutistoma* Kuroda and Shikama, 1966. Although *C. solutistoma* was described from Japan, it has been recently discovered in the Philippine Islands (D'Attilio and Emerson 1980).

The spire of *C. elvirae* is higher and convex rather than concave as in *C. caroleae*. The aperture of *C. elvirae* is restricted to a comparatively longer, narrow opening, with the inner and outer lip parallel, whereas *C. caroleae* has a broad aperture and swollen body whorl. The protoconch of *C. elvirae* consists of two and one-fourth whorls with weakly beaded cords; there is only one cord on the final whorl (D'Attilio and Emerson 1980). The protoconch of *C. caroleae* has two and one-half to three whorls, the beading on the cords is much stronger, and the final whorl has two cords. *Coralliophila solutistoma* has a heavier, larger shell with a higher spire and less inflated body whorl; the axial ribbing is much stronger and the ribbing is continuous over the entire shell. The protoconch is more coarsely beaded (D'Attilio and Emerson 1980).

Notes on Two Additional Species of *Coralliophila*

Two well-known species of *Coralliophila*, widely distributed throughout the Indo-Pacific, are discussed below. The two species are usually found in such eroded and encrusted condition that morphological characters are obscured. Hence, an adequate description of the protoconch and early whorls has been lacking in the literature. We are fortunate in having at our disposal (SDNHM) juvenile specimens of each, and we have thus appended information regarding their shell morphology, protoconch and operculum to add to a general understanding of the genus.

Coralliophila erosa Röding, 1798
Figures 32–34

This species is distributed throughout the Indo-Pacific, mostly intertidal. Morphologically it exhibits considerable inter- and intrapopulation variation. The shell is often, as the name suggests, encrusted or eroded, obscuring the finely scabrous surface. It has a characteristic sinuous outer lip, the upper portion of which is deeply concave. The operculum is thin with close concentric ridges externally; internally there are six U-shaped ridges. The protoconch is distinguished by having one and three-fourths low and weakly convex whorls; spire is depressed. An uneroded juvenile specimen (SDNHM 77174) from Hawaii is illustrated.

Coralliophila neritoidea Lamarck, 1816
Figures 29–31

This species has a distribution and habitat similar to *Coralliophila erosa*. The white shell is most often encrusted with calcareous organisms. When not encrusted or eroded, the surface of the shell is spirally scabrous. After the first two to three postnuclear whorls there often follows a rapid expansion of the body whorl. The purple aperture is less prominent in immature specimens. The operculum is a dark chocolate brown with a lateral mid-central nucleus. Internally it has a thickened ridge and four ovate ridges spaced over the remaining surface. The protoconch has two to two and one-half smooth, acutely conical whorls, followed by a whorl with a midway rib. A juvenile specimen (SDNHM 66538) is illustrated.

Acknowledgments

The following friends and collectors have contributed towards the completion of this paper: Mr. Kenneth Riley, for donating the specimens used in the description of *Hexaplex rileyi*; Mr. and Mrs. Andre DeRoy from Santa Cruz Island, Galápagos Islands, for donating specimens of *Babelomurex deroyorum*; Mr. Donald Pisor of San Diego, California, and Mr. Loyal J. Bibbey of Imperial Beach, California, for donating specimens of *Babelomurex jeanneae*; Mr. Gene Everson of Lauderhill, Florida, and Mr. Donald Pisor for contributing specimens of *Coralliophila armeniaca*; Mr. Donald Pisor and Mr. Jim Springsteen of Manila, Philippine Islands, for donating specimens of *Coralliophila caroleae*.

We are especially grateful to Mr. David K. Mulliner of San Diego, California, for the photographs used in this paper. We further thank Dr. Richard C. Brusca, Chairman, Department of Marine Invertebrates, San Diego Natural History Museum; Dr. William K. Emerson, American Museum of Natural History; and Dr. Emily H. Vokes, Tulane University, for editorial review of the manuscript. Marjorie Rea kindly typed the manuscript.

Literature Cited

Adams, A. 1853. Descriptions of several new species of *Murex, Rissoina, Planaxis* and *Eulima* from the Cumingian collection. Proc. Zool. Soc. London for 1851 19:267–272.

Adams, H. and A. 1853–54. Genera of Recent mollusca. Van Voorst, London. vol. 1, 484 pp.

Biggs, J. E. J. 1973. The marine mollusca of the Trucial coast. Bull. Br. Mus. (Nat. Hist.) Zool. London 24(8):343–421.

Blainville, H. M. 1832. Disposition méthodique des espèces récents et fossiles des genres Pourpre, Ricinule, Licorne et Concholépus de

M. de Lamarck, et description des espèces nouvelles ou peu connues, faisant partie de la collection du Muséum d'Histoire Naturelle de Paris. Nouv. Ann. Mus. d'Hist. Nat., Paris, 1: 189–263.

Carpenter, P. P. 1857. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Rep. Brit. Assoc. Adv. Sci. for 1856, pp. 159–368.

Chenu, J. C. 1859. Manuel de conchyliologie et de paleontologie conchyliologique. Paris. vol. 1, 508 pp.

Coen, G. 1922. Del genere *Pseudomurex* (Monterosato, 1872). Atti. Soc. Ital. Sci. Nat. Mus. Civico. Storia Nat. Milano 61:68–71, pl. 2.

D'Attilio, A. 1978. Catalogue of the Family Coralliophilidae. Festivus 10(10):69–96.

———. 1979. Corrections and additions to the Catalogue of the Family Coralliophilidae. Festivus 11(10):83–85.

———. 1983. Concerning the identity of *Murex pagodus* A. Adams, 1853. Festivus 15(1): 2–4.

D'Attilio, A., and W. K. Emerson. 1980. Two new Indo-Pacific Coralliophilid species (Gastropoda, Muricacea). Bull. Inst. Malac. Tokyo 1(5): 69–73.

D'Attilio, A., and G. Radwin. 1973. The intritacalx, an undescribed shell layer in mollusks. Veliger 13(4):344–347.

Emerson, W. K., and A. D'Attilio. 1963. A new species of *Latiaxis* from the western Atlantic (Mollusca, Gastropoda). Amer. Mus. Novitates 2149:1–9.

———, and ———. 1970. Three new species of Muricacean gastropods from the eastern Pacific. Veliger 12(3):270–274.

Gmelin, J. F. 1791. Caroli a Linne Systema naturae per regna tria naturae. Ed. 13. Leipzig, Germany. vol. 1, pt. 6, pp. 3021–3910.

Iredale, T. 1912. New generic names and new species of marine Mollusca. Proc. Malac. Soc. London for the year 1914 10:217–228.

———. 1915. A commentary on Suter's "Manual of New Zealand Mollusca." Trans. and Proc. Royal Soc. of New Zealand 47:417–497. Wellington.

Kiener, L. C. 1836. Spécies général et inconographie des coquilles vivantes comprenant la collection du Muséum d'Histoire Naturelle de Paris . . . . Genre Pourpre (*Purpura*, Lam.), pp. 1–149.

Kosuge, S. 1979. Descriptions two new subgenus [sic] and seven new species of the genus *Latiaxis* (Gastropoda, Mollusca). Bull. Inst. Malac. Tokyo 1(1):3–8.

Kuroda, T., and T. Shikama, in T. Shikama. 1966. On some new *Latiaxis* and *Coralliophila* in Japan. Venus 25(1):21–25.

Lamarck, J. B. P. A. de M. de. 1816. Tableau encyclopédique et méthodique des trois règnes de la nature. Liste. 16 pp.

Linné, C. von. 1758. Systema naturae. Stockholm. 10th ed. vol. 1, pp. 1–824.

———. 1767. Systema naturae. Stockholm. 12th ed. Vol. I, Pt. II—Mollusca. pp. 1081–1267.

Martens, E. von. 1874. Uebereinige Sudafrikanische mollusken. Jahrb. Deutsch Malak. Gesell. pp. 119–146.

Oldroyd, I. S. 1929. Description of a new *Coralliophila*. Nautilus 42(3):98–99.

Perry, G. 1811. Conchology or the natural history of shells, containing a new arrangement of the genera and species. Wm. Miller, London.

Rafinesque, C. S. 1815. Analyse de la nature ou tableau du univers et des corps organises. Barravecchia, Palermo.

Requien, E. 1848. Catalogue des coquilles de l'Ile de Corse. Avignon.

Robertson, R. 1970. Review of the predators and parasites of stony corals with special reference to symbiotic prosobranch gastropods. Pac. Sci. 24(1):43–54.

———. 1980. *Epitonium millecostatum* and *Coralliophila clathrata*: Two Prosobranch gastropods symbiotic with Indo-Pacific Palythoa (Coelenterata: Zoanthidae). Pac. Sci. 34(1):1–17.

Röding, P. F. 1798. Museum Boltenianum. Hamburg. 199 pp.

Smith, E. A. 1903. A list of species of mollusca from South Africa, forming an appendix to G. B. Sowerby's "Marine Shells of South Africa." Proc. Malac. Soc. London 5:354–402.

Sowerby, G. B. II. 1834–41. The Conchological Illustrations, *Murex*. Sowerby, London. pls. 58–67, 1834; pls. 187–199, 1841.

Tapparone-Canefri, C. M. 1875. Viaggio dei . . . O. Antinori, O. Beccari ed. A. Issel nel Mar. Rosso . . . 1870–71. Studio monografico sopra il Muricidi, etc. Ann. Mus. Civ. Stor. Nat. Genova 7:560–640.

Thiele, J. 1929–35. Handbuch der Systematischen Weichtierkunde, Jena: Gustav Fischer, Bd. I, Tiel I, 376 pp.

Ward, J. 1965. The digestive tract and its relation to feeding habits in the stenoglossan prosobranch *Coralliophila abbreviata* (Lamarck, 1816). Canadian Jour. Zool. 43:447–464.

Woolacott, L. 1954. New shells from New South Wales. Proc. Roy. Soc. New South Wales, Zoology 1952–53: pp. 37–39.

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The Fossil Leptostracan *Rhabdouraea bentzi* (Malzahn, 1958)

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Abstract. The type material of the only known fossil leptostracan phyllocarid, *Rhabdouraea bentzi*, is reexamined. This species was originally placed in the genus *Nebalia*. The distinctive caudal rami and the form of the carapace, however, require separate generic and familial status for this Permian material. A redefinition of the living family Nebaliidae is also provided.

Introduction

The fossil record of the Phyllocarida has always presented problems for phylogenetic analysis because of the incomplete nature, generally, of the fossils (Rolfe 1981). This has been especially vexing for the assessment of the living order Leptostraca where, with a single exception, fossils are non-existent. Malzahn (1958) described *Nebalia bentzi* on the basis of a single specimen from the Upper Permian Zechstein of West Germany. Further discussion of this species was provided by Glaessner and Malzahn (1962). Initial assignment of this material to the living genus *Nebalia* reflected a conservative approach pending the discovery and study of more and better material. Unfortunately, despite continuing efforts at collection and study of this fauna by the junior author, no additional specimens have turned up. However, restudy of the known material has enabled us to clarify the relationship of this Permian species to the living leptostracans.

Systematic Paleontology

Class Malacostraca Latreille, 1806
Subclass Phyllocarida Packard, 1879
Order Leptostraca Claus, 1880
Family Rhabdouraeidae n. fam.

Diagnosis.—Same as that of the genus.
Type genus.—*Rhabdouraea* n. gen.

Rhabdouraea new genus

Diagnosis.—Carapace short, not covering abdomen. Caudal rami rod-like, at least as long as abdomen.
Etymology.—From the Greek *rhabdos* (=rod) and *uraea* (=tail), gender feminine.
Type species.—*Nebalia bentzi* Malzahn, 1958.

Rhabdouraea bentzi (Malzahn, 1958)

Diagnosis.—Since only one species is known, the diagnosis of the species is the same as that of the genus.

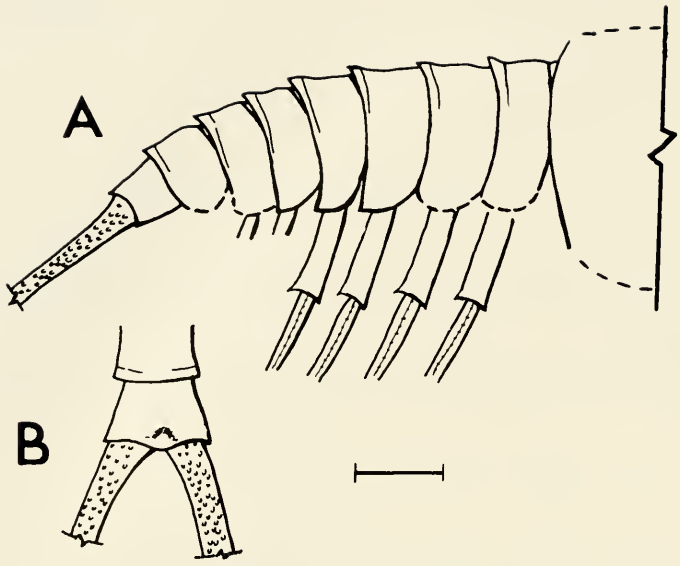

FIGURE. 1. Partial reconstruction of *Rhabdouraea bentzi* (Malzahn). A.) lateral view of abdomen. B.) dorsal view of telson and caudal rami. Scale 2 mm.

Holotype.—Z45, in the collection of the Niedersächsisches Geologisches Landesamt, Hannover. From a depth of 280–282 m, Shaft 4, of the Friedrich-Heinrich Mine, near Ort Hoerstgen, Niederrhein, German Federal Republic. Zechstein 1, Upper Permian.

Description.—The posterior margin of the carapace is visible on the type, and covers the posterior aspect of the thorax while leaving the anterior pleomeres exposed (Figs. 1 and 2). The pleomeres are subequal, each about 0.7 mm in length. The posterior margin of the abdominal tergites are raised as a slight ridge. The abdominal pleura are rounded anteriorly and somewhat acuminate posteriorly. At least the four anterior pleopod protopods are long and robust; the fifth and sixth are present, appear to be somewhat smaller than those of the anterior limbs, but cannot be clearly discerned because of the preservation of the specimen. The seventh pleomere appears to lack appendages. The distal branches of the anterior pleopods are robust, and marked by a line of lateral pits (which may have been sockets of marginal setae). The telson is only slightly shorter than the pleomeres, and with a slight fossa or depression on the dorsal surface between the bases of the caudal rami. The telson bears terminally a set of large, rod-like, papillose caudal rami. The length of these rami cannot be determined exactly since their distal ends are broken off. However, the longer ramus (now broken in two pieces) is at least 3.5 mm and indicates the rami were probably at least as long as the abdomen.

Family Nebaliidae Baird, 1850

Diagnosis.—Carapace generally large, covering anterior pleomeres as well as the thorax. Caudal rami relatively short, as flaps with marginal setae.

Type genus.—*Nebalia* Leach, 1814.

Discussion

The two distinct features of *Rhabdouraea bentzi* are the short carapace and the long, rod-like caudal rami, so diagnostic in fact as to warrant separate generic and familial status for this species.

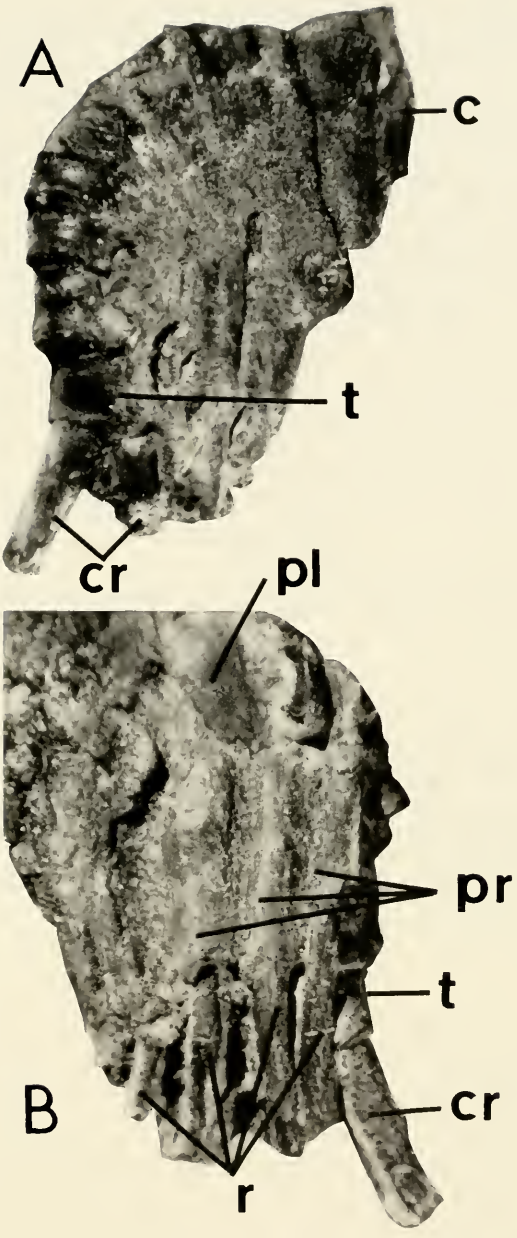

FIGURE 2. *Rhabdouraea bentzi* (Malzahn), holotype, Z45. A.) Right side [right caudal ramus visible on original illustrations since broken off, but still retained with specimen], 10x. B.) Left side, closeup of anterior pleopods and caudal ramus, 16x; c—carapace, cr—caudal ramus, pl—pleuron of second pleomere, pr—pleopodal protopods, r—distal rami of pleopods, t—telson.

The living leptostracans typically have a large carapace that completely encloses the body, except for the posteriormost portions of the abdomen, and lobate, setose caudal rami. The only exception to these features occurs in the genus *Nebaliopsis*. This pelagic form has the posterolateral aspect of the carapace truncate, exposing the pleomeres and ventral portions of the posterior thoracomeres. In addition, the caudal rami in *Nebaliopsis* are thin and leaf-like. These features are prompting Hessler (in prep.)

to place *Nebaliopsis* in its own family, separate from the benthic nebaliid genera. The differences noted on *Rhabdouraea,* incomplete though the fossil is, are of a magnitude at least as great as that which separates *Nebaliopsis* from *Nebalia, Paranebalia,* and *Nebaliella,* and thus justify separating this Permian taxon by itself.

All the living nebaliids, benthic or pelagic, have relatively short or modest sized caudal rami with setose margins. These rami function in a manner analogous to uropods, and assist the animal in swimming. The very long, papillose, rod-like rami in *Rhabdouraea* are unlike any of those seen among leptostracans, and are more akin to those seen in notostracan branchiopods.

Several features of *Rhabdouraea bentzi* ally this species to the leptostracan phyllocarids, viz., the four well-developed anterior pleopods, the two apparently small posterior pleopods, the lack of the seventh pleopods, the robust pleopod protopods, the lateral row of pits on the pleopod distal branches, and the telson not developed dorsally between the caudal rami. The recognition of the separate familial status of *Rhabdouraea bentzi* seconds the suspicions of Rolfe (1969) that this species was not referable to any of the Recent genera. This requires an emendation of the diagnosis of the living family Nebaliidae noted above.

Acknowledgments

Drs. Robert Hessler and Ian Rolfe examined the material and offered valuable counsel on the taxonomic issues. Work was supported in part by NSF grant DEB 79-03602 (FRS).

Literature Cited

Malzahn, E. 1958. Eine neuer jungpaläozoischer Krebs aus dem niederrheinischen Zechstein. Zeit. deutsch. geol. Ges. 110:352–359.

Glaessner, M. F., and E. Malzahn. 1962. Neue Crustaceen aus dem niederrheinischen Zechstein. Fortschr. Geol. Rheinld. u. Westf. 6:245–264.

Rolfe, W. D. I. 1969. Phyllocarida. Pp. R296–R331 *in* R. C. Moore (ed.). Treatise on Invertebrate Paleontology, Part R, Arthropoda 4(1), Geol. Soc. Am. and Univ. Kansas Press, Lawrence.

———. 1981. Phyllocarida and the origin of the Malacostraca. Geobios 14:17–27.

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Phylogeny, evolution and biogeography of the marine isopod Subfamily Idoteinae (Crustacea: Isopoda: Idoteidae)

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Abstract. The patterns of spatial distribution attained by the genera of Idoteinae are discussed in light of a cladistic analysis of the suborder Valvifera and the subfamily Idoteinae. A schematic pattern analysis technique is demonstrated and reveals the probability of multiple origins of similar pleonal morphologies among various genera of Idoteinae. Reduction in the maxillipedal palp has occurred numerous times within the Idoteinae, while loss of the biramous uropodal condition has probably occurred twice. A geographic cladogram of temperate Gondwanan shores is proposed. An evolutionary-biogeographic narrative is presented, in which a set of hypotheses is developed to describe the history of the Idoteinae in time and space. The subfamily Idoteinae appears to form two principal lines of descent, both arising in the Triassic or Jurassic. One of these lines remained closely tied to the Southern Hemisphere (primarily Old World) temperate marine shores from which the Idoteinae is derived. The other line invaded the Northern Hemisphere and various New World environments, and more recently (Cenozoic) underwent a radiation in the American tropics. The success of this latter lineage (e.g., *Erichsonella, Eusymmerus, Parasymmerus, Cleantioides*) may be due to certain morphological and life history adaptations not found in New World species of the former line (e.g., *Idotea, Synidotea*). The Valvifera probably originated in the temperate Southern Hemisphere, at least by Permean/Triassic times. Global distribution patterns of some genera can be ascribed most parsimoniously to vicariance processes, and in others to dispersal, ecological phenomena, or a combination of processes. Other factors have apparently also affected modern distributional patterns of idoteine genera, for example, extinctions. Biogeographical data can be used to elucidate viable alternative cladistic hypotheses to those generated solely on parsimonious patterns of synapomorphy. Biogeographic data can also be used, in conjunction with the cladogram, to identify probable ancestral taxa.

Introduction

Few groups of marine invertebrates have enjoyed analysis by cladistic techniques, despite the current popularity of the method. The only previous attempt to examine the phylogenetic relationships of an isopod taxon by strict cladistic (Hennigian) methodology was that of Williams (1970), who analyzed the relationships of North American epigean species of *Asellus* (Asellota); but, as was common with early attempts at Hennigian analyses, he used a weakly defined method of character state polarity assessment. Despite this, he was still able to construct a very plausible phylogenetic hypothesis, or cladogram, for the 14 species he treated.

One reason for the paucity of cladistic studies on marine invertebrates is the necessity to work with a group whose taxonomic relationships are reasonably well known within the context of the larger hierarchical taxon to which the study group belongs. Without this knowledge, an assessment of character polarity is difficult to obtain, and without polarities, construction of both cladograms and phylogenetic (evolutionary) trees must be based on speculatively generated hypothetical ancestors (expressed or implied). Although several marine invertebrate taxa are well understood systematically (e.g., certain families of molluscs, crabs, barnacles), the great majority are not. Several crustacean isopod groups are also well understood in this regard. The subfamily Idoteinae (suborder Valvifera; family Idoteidae) is one such group.

The present study attempts to answer questions about the evolutionary history of the Idoteinae using cladistic techniques. Specific questions addressed are: What are the

phylogenetic patterns and relationships of the genera of Idoteinae? What are the spatial patterns and relationships of the genera of Idoteinae? What evolutionary history is suggested when these patterns are compared to one another and to the earth's geological and ecological history? Previous studies on these topics include comments on the phylogeny and biogeography of the genus *Idotea* by Menzies (1950*a*); on the genus *Synidotea* by Menzies and Miller (1972); and on the comparative morphology of the valviferan higher taxa in general by Sheppard (1957). A review of the distribution of shallow-water idoteine species in the northeastern Pacific was given by Brusca and Wallerstein (1979*b*), and a discussion of the possible ecological and historical mechanisms regulating distribution and latitudinal trends in morphology and behavior in that taxon is provided by Wallerstein and Brusca (1982).

Methods

The methods used in this study are largely summarized in 3 recently published books (Eldredge and Cracraft 1980, Nelson and Platnick 1981, Wiley 1981). However, even the principal spokesmen of current cladistic theory are not without disagreement on both details of procedure and certain underlying philosophical issues. As Eldredge and Cracraft (1979) point out, "No two cladists agree with each other (or, for that matter, with Willi Hennig) on every point, and this 'school' of systematics is no more a monolith than that of the more traditional 'evolutionary taxonomy'." The overall concept of cladistic or "phylogenetic" analysis has evolved considerably since Hennig (1966), and indications are that it will continue to change for some time to come. For these reasons, and others, I offer the following position statements.

While the present study is cladistic in nature, it is my opinion that such analyses are most useful as investigatory techniques and do not represent the final word on phylogeny. The most powerful (and important) aspect of cladistic methodology is its ability to posit and define monophyletic groups in an unambiguous and testable manner. Synapomorphy patterns, however, do not constitute the sole source of phyletic information on a taxon, but rather must be compared to other kinds of data and analyses when constructing phylogenetic trees, evolutionary scenarios, AND classifications. A cladogram depicts only a sequence of character appearances, which may or may not correspond to speciation events (Hull 1979). There appear to be 4 principal products that can result from phylogenetic analyses: cladograms, phylograms (evolutionary trees), evolutionary scenarios, and classifications. The cladogram should be viewed as a "best guess" in the face of uncertainty (Felsenstein 1973, Harper 1979, Hull 1979, Simberloff et al. 1981, Endler 1982), and information contained in any of these other products of phylogenetic analyses can legitimately be used to improve any other, including the cladogram itself (Hull 1979). In the present study I construct a cladogram, a phylogram, and an evolutionary scenario for the subfamily Idoteinae, and use the latter two products to shed new light on, and make ammendments to, the cladogram.

Nomenclature and general terminology are taken from current literature on valviferan isopods (see above references). Morphological structures discussed in this paper are illustrated in Fig. 1. Analysis of character polarity is based on out-group analysis (see Eldredge and Cracraft 1980, de Jong 1980, and Watrous and Wheeler 1981). I believe that out-group comparisons need not be rigidly constrained by nomenclatural rank or Linnean hierarchical structure, but are applicable at all levels of a cladogram. Though parsimony is a potent methodological tool, it is primarily a method of logical analysis, not a biological law or principle. Application of parsimony should be an initial technique, or one to be used in the absence of other data. To continue to hold to the

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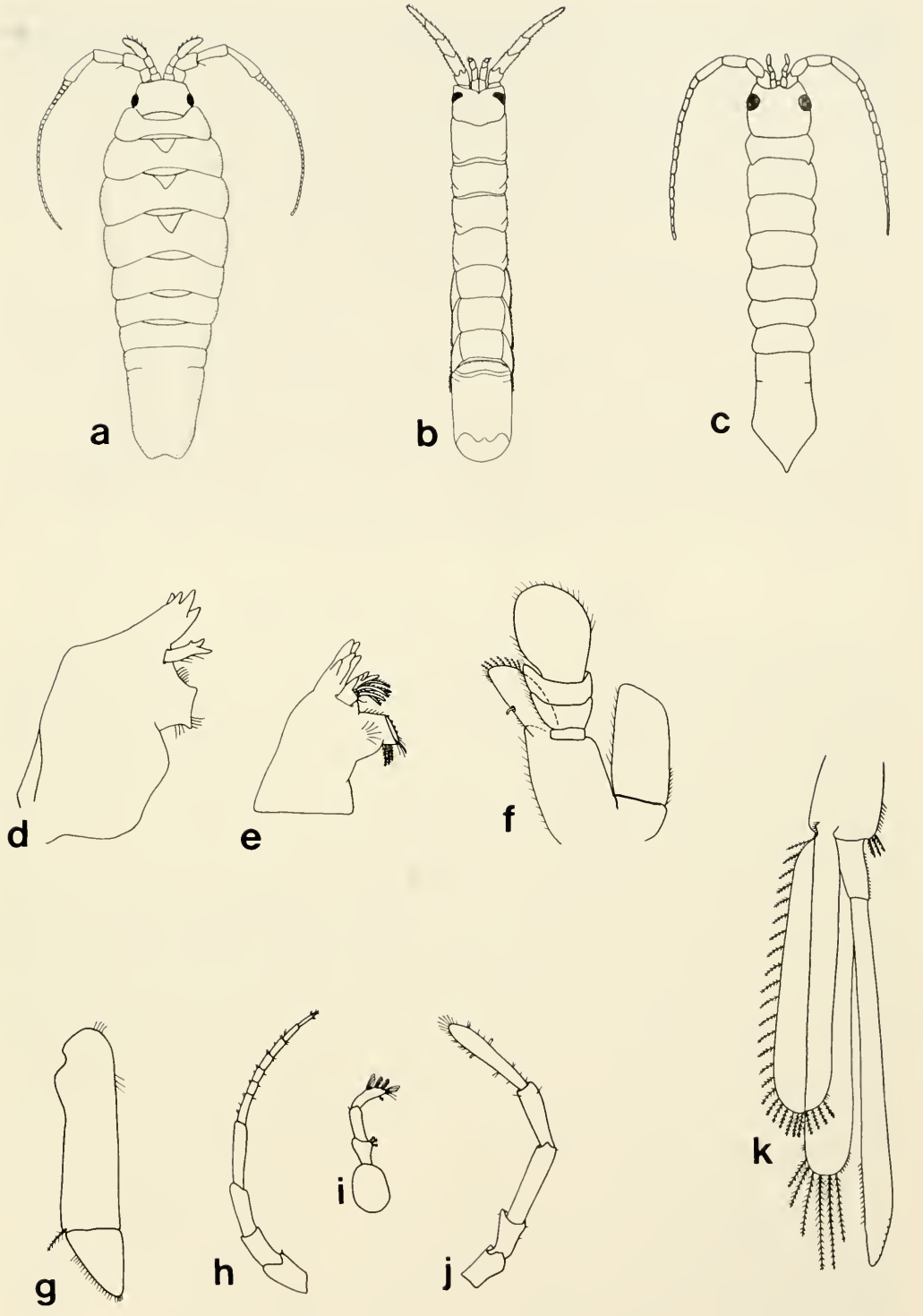
Figure 1. Aspects of the morphology of idoteid isopods discussed in the text. **a**, *Synidotea harfordi*; note multiarticulate flagella on antennae 2 and 0+1 pleonal morphology. **b**, *Cleantioides occidentalis*; note uniarticulate (clavate) flagellae on antennae 2 and 3+1 pleonal morphology. **c**, *Colidotea findleyi*; note multiarticulate flagellae on antennae 2 and 0+1 pleonal morphology. **d**, Mandible of *Eusymmerus antennatus*;



note large 4-toothed incisor, smaller lacinia mobilis, and stout molar process. **e,** Mandible of *Colidotea findleyi*; note 5-toothed incisor, large lacinia mobilis, and stout molar process. **f,** Maxilliped of *Colidotea findleyi*; note 4-articulate palp. **g,** Uniramous uropod of *Colidotea findleyi*. **h,** Antenna 2 of *Colidotea findleyi*; note multiarticulate flagellum. **i,** Antenna 1 of *Colidotea findleyi*; note uniarticulate flagellum. **j,** Antenna 2 of *Erichsonella cortezi*; note uniarticulate (clavate) flagellum. **k,** Pleopod 2 of *Erichsonella cortezi* (male); note appendix masculinum.

"simplest" explanation (i.e., the shortest cladogram) in the face of biological evidence indicating a less parsimonious but more biologically reasonable explanation is both nonscientific and an abuse of the tool. There is little point in creating a falsifiable hypothesis if one does not accept all forms of data that can falsify it. In this regard I agree with Kitts (1981) that phylogenetic patterns (and hence analyses) ARE historical in nature and this involves describing the real world; one could not be writing history if one supposed every relationship between events to have transpired in the "most direct" manner. Whether or not any particular phylogeny is parsimonious is something to be found out in the course of a historical investigation, it is not something to be assumed.

Finally, my technique for the historical biogeographic analysis follows the hypothetico-deductive method, primarily as described by Morse and White (1979). I assume no particular paradigm to be of overriding importance, but rather attempt to interpret the patterns of characters and distributions in the most parsimonious (biological parsimony) fashion possible. McDowall (1978) was, of course, correct in noting that one can never know with certainty whether any given individual component track is the product of vicariance or dispersal. However, that both phenomena exist in nature can hardly be denied, and it has been my task in the present study to decide, where possible, which of these two phenomena (or others) produced the biogeographic patterns seen today in the genera of Idoteinae. Needless to say, I have been severely hampered in this regard by the absence of cladograms for other coastal marine taxa.

Higher Classification of the Order Isopoda and the Suborder Valvifera

Out-group analysis requires acceptance of some higher level classificatory structure before statements regarding the relationships of lower, inclusive taxa can be made. For the purposes of this study, I accept the monophyletic nature (*sensu* Hennig, 1966) of three taxa: the order Tanaidacea, the order Isopoda, and the suborder Valvifera. The monophyletic nature of these distinct taxa are, to my knowledge, unquestioned.

While the nature of the primitive isopod body plan (presented below) is generally agreed upon, the relationships of the 9 isopod suborders are unknown and fraught with speculation (see Schultz 1979 for recent summary comments). Various authors have described the nature of the primitive or ancestral isopod morphotype, which is characterized by the following combination of characters: carapace wanting; pereopods uniramous; respiratory structures (heart and branchial surfaces) primarily abdominal; pereopodal coxae forming marginal plates on pereonites; first and second antennae with multiarticulate flagella; mandible with a multiarticulate palp; appendix masculina present only on second pair of pleopods; uropods biramous (probably attached terminally or subterminally to telson or pleotelson, although some authors suggest a lateral attachment vis-à-vis the cirolanoids); eyes entirely sessile; all pereopods more or less similar; pereon of 7 free somites (thoracomeres 2–8); pleon of 6 free somites and a telson (or possibly 5 free somites and a pleotelson); maxilliped with a large basal endite and reduced endopodal articles (the latter forming the 5-articulate palp); maxilliped with a small, ovate, nonbranchial epipodite (the "endognath"); penes and opening of vas deferens on thoracomere 8; simple foregut; and maxillary glands present in adults.

This generalized ancestral isopod plan was first developed in the early studies of Bate and Westwood (1861–1868), Stebbing (1893), and Calman (1909), and more recently by Schram (1974) and Hessler et al. (1979). The concept of this morphotype is supported by fossil data as well as by comparison with other peracarid and malacostracan taxa. It is also compatible with all three "competing" hypotheses of extant primitive isopod morphotypes (i.e., cirolanoid, phreatoicid, asellote).

The Valvifera stand apart as perhaps the most distinct of the isopod suborders in several regards. Important features distinguishing the valviferan body plan are (see Fig. 1): (a) coxae of thoracic legs (pereopods) with both dorsal and ventral plates, the latter extending over the sterna; (b) uropods attached laterally on pleotelson, but modified

to form ventral opercular plates covering the pleopods; (c) vas deferens (and penes) opening on abdomen of male, rather than on thorax as in all other isopods, excepting the Oniscoidea (i.e., on pleonite 1 or on the articulation of pleonite 1 and thoracomere 8); (d) flagella of first antennae reduced to one or a few vestigial articles; (e) pleon of 4 or fewer free somites (plus the pleotelson); (f) uropods biramous or uniramous; (g) maxillipedal palp of 3–5 articles; (h) second antennae uniramous, flagellum multiarticulate or uniarticulate; (i) mandible with or without a 3-jointed palp. Attributes (a) and (b) are unique synapomorphies that distinguish the Valvifera from all other isopod taxa; attributes (c) through (f) are valviferan synapomorphies that also appear in one or more other isopod suborders (apparent convergences).

The current classification of the isopod suborder Valvifera is as follows:

Order Isopoda Latreille, 1817
  Suborder Valvifera Sars, 1882
    Family Hologнathidae Thomson, 1904
    Family Idoteidae Fabricius, 1798
      Subfamily Idoteinae Dana, 1852
      Subfamily Parachiridoteinae Elkaim and Daguerre de Hureaux, 1976
      Subfamily Glyptonotinae Miers, 1881
      Subfamily Chaetilinae Dana, 1852 (=Macrochiridoteinae Nordenstam, 1933)
      Subfamily Mesidoteinae Racovitza and Sevastos, 1910
    Family Xenarcturidae Sheppard, 1957
    Family Arcturidae G. W. Sars, 1897
    Family Amesopodidae Stebbing, 1905
    Family Pseudidotheidae Ohlin, 1901

The relationships of the 6 valviferan families have long been unclear. The only cogent discussion of the topic was that of Sheppard (1957). The cladogram in Fig. 2 depicts the best arrangement that I have been able to devise for these families, being the most parsimonious, and admitting no convergences, parallelisms or reversals. A convincing higher level classificatory scheme of the 9 isopod suborders does not presently exist, and carcinologists disagree over the relationships among these taxa. For this reason, the Tanaidacea was used as an out-group to construct the cladogram of valviferan families (Fig. 2). Tanaidacea is the peracarid order "traditionally" (Schram 1981) taken to be the most probable sister-group to the Isopoda (also see Siewing 1963 and Fryer 1964). Whether or not it is the actual sister-group of the isopods is unimportant for its use in out-group comparison, however, as it is clearly a closely related taxon within the unified peracarid line. Character polarity assessments based on tanaids were compared to those obtainable by using the Amphipoda, Cumacea and hypothetical ancestral isopod as out-groups and no changes in polarity were required when these other groups were used in place of tanaids.[1] A step-by-step discussion of the cladogram of valviferan families follows, the numbering in the text following that of Fig. 2.

Tanaids are united to the isopods only by possession of their peracarid attributes, the most obvious of these being: (a) pereopodal coxae with thin ventral plates (oostegites) that form a female brood pouch for the developing young; (b) mandibles with lacinia mobili in adult stages of life cycle, and (c) young released from the marsupium in subadult "mancoid" stage. At this level of analysis these attributes are symplesiomorphies; I know of no synapomorphies unique to the tanaids and isopods.

The Isopoda are united by the features listed above for the primitive isopod morphotype. The first 4 of these are synapomorphies, as follow: (1) carapace wanting (vs. present in tanaids); (2) pereopods uniramous (vs. retaining vestiges of exopods); (3) respiratory structures (branchial pleopods and heart) primarily abdominal (vs. thoracic); (4) pereopodal coxae forming marginal plates on pereonites (vs. not forming plates).[2]

The Hologнathidae shares in common with its sister-group (the remaining 5 valviferan families) the 4 valviferan synapomorphies listed earlier: (5) pereopodal coxae form ventral (sternal) plates; (6) uropods modified into opercular plates covering pleo-

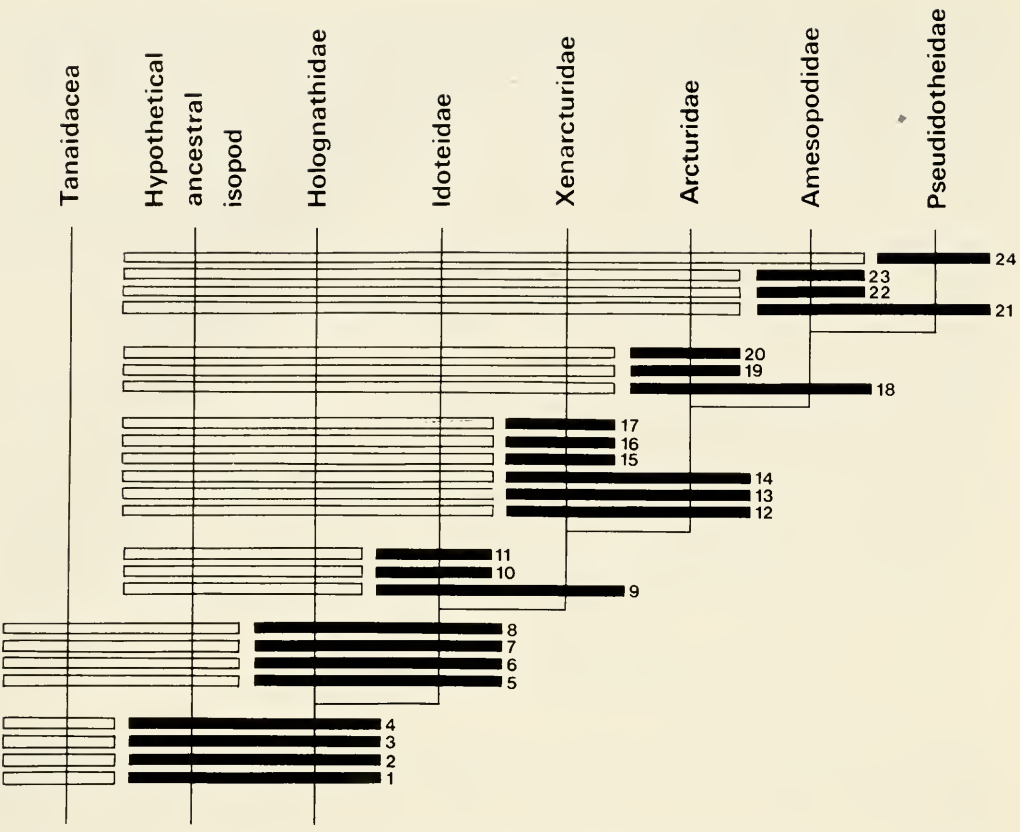


FIGURE 2. Cladogram of families of Valvifera. Closed boxes indicate apomorphies; open boxes plesiomorphies. Numbering of characters corresponds to text discussion.

pods; (7) vas deferens and penes opening on abdomen of male, rather than on thorax; (8) flagella of first antennae reduced to one or a few vestigial articles. The Hologhathidae is a monotypic family containing but one species, *H. stewarti* (Filhol). It cannot be distinguished by an autapomorphy of its own, although it stands apart from all other species in the suborder Valvifera by its retention of a palp on the mandible, as well as numerous other primitive attributes (e.g., biramous uropods, 5-articulate maxillipedal palp, pleon of 4 free somites plus the pleotelson). *Hologhathus* may be considered a relict taxon within the Valvifera. Nordenstam (1933) long ago recognized the lack of apomorphies in *Hologhathus,* suggesting that it might best be incorporated into the Idoteidae. Were this done, however, *Hologhathus* would probably have to be ranked as a sixth subfamily, rather than included in the Idoteinae as Nordenstam suggested. The presence of 4 free pleomeres places this genus at a position ancestral to both the Idoteinae and the Glyptonotine-group discussed below (see Fig. 3). The remaining valviferan families are thus united by the loss of the mandibular palp (9). Clearly, were one to place *Hologhathus* in the Idoteidae, characters 5–8 would become synapomorphies uniting Idoteidae to all other valviferan families.

The Idoteidae stand apart as the only family in which the uropods may be reduced from the primitive biramous state to a uniramous condition (10), and in which a reduction of the maxillipedal palp takes place (11). The Idoteidae have been characterized by two other "synapomorphic trends": trends towards fusion of the pleonites and towards fusion (or loss) of the flagellar articles on the second antennae. These reductions, however, are convergent to patterns that also occur in other valviferan families and thus have not been used to construct the cladogram (Fig. 2). The Idoteidae

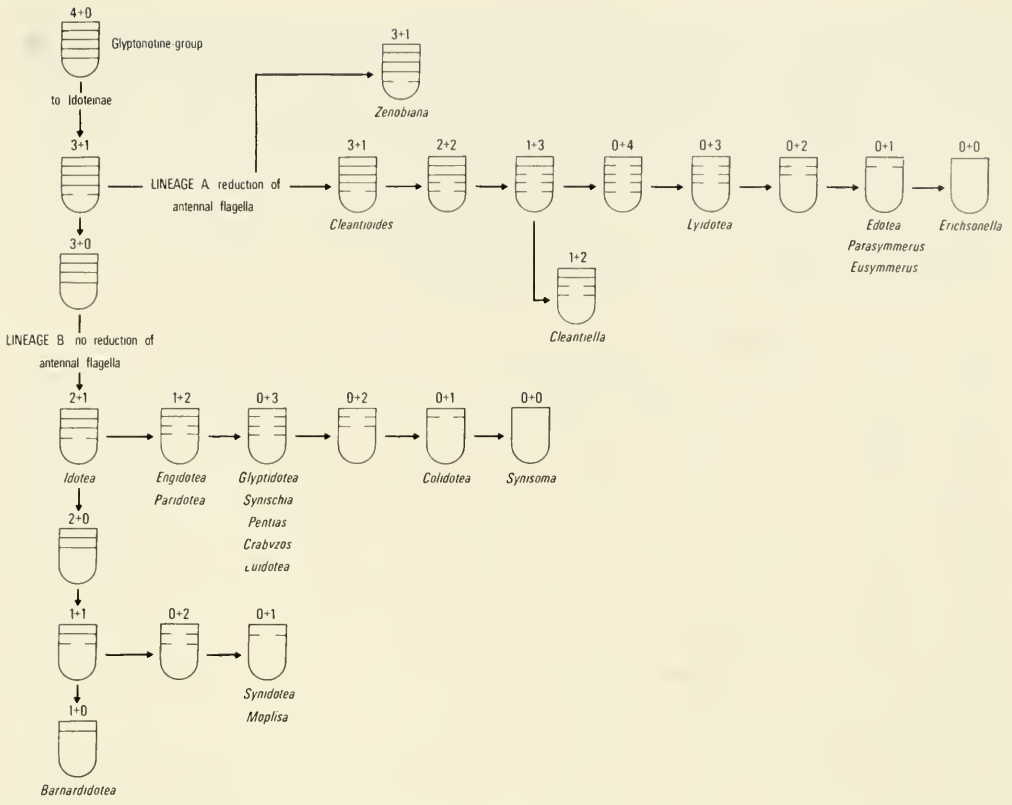


FIGURE 3. Schematic representation of possible phylogenetic pathways for pleonal fusion in the Idoteinae. Pleonal formulas are written above pleonal diagrams and indicate number of free and number of fused pleomeres. Genera assigned to given pleonal morphology are indicated below diagrams. See text for discussion.

stands out most strikingly from the 4 families that comprise its sister-group in the retention of numerous plesiomorphic attributes (e.g., free penes retained in 4 of the 5 subfamilies; free cephalon; one pair of appendix masculina, on the second pleopods). Racovitza and Sevastos (1910) long ago recognized the primitive nature of the Idoteidae, regarding it as an "ancient" family. The Idoteidae was the first valviferan family to be described, subsequent families being distinguished from it by elucidation of new characters acquired outside the Idoteidae. Thus, historically a diagnosis of the Idoteidae has been developed largely upon absence of characters (a phenomenon common among older taxa). The discovery of new distinguishing attributes (apomorphies) for the Holognathidae and Idoteidae is clearly needed and will provide important data for testing the hypotheses contained in the cladogram.

The Xenarcturidae and its sister-group (Arcturidae-Amesopodidae-Pseudidotheidae) are distinguished by the following synapomorphies: (12) first pleopods of males bearing "accessory appendix masculina" (in addition to the true appendix masculina of the second pleopods); (13) cephalon fused medially to pereonite I (second thoracomere); (14) peduncle of first pleopods greatly elongated. The Xenarcturidae is a monotypic taxon distinguished by the following autapomorphies: (15) pereonites I–IV with lateral margins expanded into large plates covering bases of pereopods; (16) second antennae with flagella reduced to single articles; and (17) flagella of second antennae directed towards mouth, rather than away from buccal field.

The Arcturidae and its sister-group (Amesopodidae-Pseudidotheidae) are distinguished by a synapomorphy in the functional grouping of the pereopods (18). Only in these taxa are pereopods I–IV similar and directed forward to form a functional group

distinct from pereopods V–VII. In all other valviferan taxa the pereopodal functional grouping is I–III and IV–VII. Arcturidae is distinguished by two synapomorphies: (19) the unique body shape (cylindrical or tubular, often geniculate), and (20) having pereonite IV generally manifestly enlarged or elongated.

The Amesopodidae and Pseudidotheidae are distinguished by the synapomorphic condition of having pereonites II–IV grossly enlarged (21). Amesopodidae is a monotypic family (*A. richardsonae* Stebbing, 1905) distinguished by the autapomorphies of highly reduced second pereopods (22), and the complete loss of pereopods III and IV (23). Pseudidotheidae contains two genera distinguished by the synapomorphy of fusion of the first two articles of the peduncle of the second antennae (24).

The Family Idoteidae and the Subfamily Idoteinae

The systematic history of the family Idoteidae can be traced through the following works: H. Milne Edwards (1840), Dana (1853), Bate and Westwood (1868), Harger (1880), Miers (1881), Chilton (1890), Ohlin (1901), Richardson (1905*a*), Stebbing (1905), Collinge (1917), Barnard (1920), Nordenstam (1933), Menzies (1950*a*), Sheppard (1957), and Menzies and Miller (1972). The American idoteid fauna is well known, largely due to the work of Dana (1853), Harger (1880), Benedict (1897), Richardson (1899*a, b,* 1900, 1901, 1904, 1905*a, b,* 1909), Hatch (1947), Menzies and Waidzunas (1948), Menzies (1950*a, b*), Menzies and Bowman (1956), Menzies and Frankenberg (1966), Menzies and Miller (1972), and Brusca and Wallerstein (1977, 1979*a,b*). All species of Idoteidae are marine, although two species of the subfamily Mesidoteinae also extend their distributions into fresh water. *Saduria* (=*Mesidotea*) *entomon* has been found in several deep Scandinavian lakes, and *Austridotea lacustris*[3] occurs from the littoral zone to fresh water rivers and lagoons in New Zealand.

The subfamily Idoteinae contains 22 valid genera (Table 1). The great majority are shallow-water and, for the most part, intertidal species. Few species are restricted to depths greater than 30 m. For the past 150 years (since the work of Brandt 1833 and H. Milne Edwards 1840) studies on this group have consistently found that the use of a few clearly defined characters provided a basis for a classification that has been both stable and reliable. Thus most idoteine genera are clearly defined, unambiguous, and easily distinguished from one another. As will soon be seen, however, not all idoteine genera can be defined by unique apomorphies. The few genera that are not clearly differentiated from one another comprise 2 small groups of largely monotypic, Southern Hemisphere genera that are in need of reexamination. Principal characters used to distinguish the idoteine genera are external and easily recognized, as follows.

Uropods.—The uropods of Idoteinae are either biramous or uniramous. The primitive biramous condition, while being clearly distinct from the uniramous condition and hence useful in pattern analysis, is not understood ontogenetically (see Calman 1909, Racovitza and Sevastos 1910, Tait 1917, Nordenstam 1933, and Menzies and Miller 1972). Loss of one uropodal ramus has occurred at least twice among the valviferan families, in the Idoteidae (subfamily Idoteinae) and again in a single species of Arcturidae (*Microarcturus digitalis* Nordenstam 1933). Whether or not these separate losses were by the same "mechanism" is not known.

Pleon.—Isopod taxa are characterized by varying degrees of fusion of the pleomeres and telson. Although trends towards fusion of pleomeres are evident throughout the Isopoda and occur in every suborder, no one has yet attempted to analyze these morphoclines in a systematic fashion (Fig. 3). In the Valvifera, there are always four or fewer free pleomeres, plus the pleotelson. The term "pleotelson" refers to that region of the pleon consisting of the telson and its fused pleomeres. For many years, the pattern of discrete character states manifested by fusion of pleomeres in the idoteine genera has been taken to represent a morphocline that is a sequence of phenotypes presumed to reflect the probable evolutionary pathway of descent. The polarity or direction of this morphocline is clearly shown by out-group analysis to be towards levels of increasing pleomere fusion. Fusion of the pleomeres is often (but by no means always) indicated by the presence of partly free lateral margins, distinguishable by the presence

TABLE 1. Summary of "traditional characters" used to differentiate the genera of Idoteinae (from Menzies and Miller 1972; with corrections). See text for additional characters. *Edotea* includes the synonym *Epelys*, and *Zenobiana* includes the synonym *Cleantis*. *Erichsonella* includes the synonyms *Erichsonia* Dana and *Ronalea* Menzies and Bowman. Pires (pers. comm.) has a manuscript in preparation in which she intends to remove the monotypic genus *Ronalea* from synonymy with *Erichsonella*, based on the alleged presence of a single pair of lateral incisions in *R. pseudoculata* (Boone). I have not examined *R. pseudoculata* myself. Such a change would require a minor revision in the cladogram (Fig. 17b), by adding *Ronalea* as a fork at the tip of the line leading to *Eusymmerus*, making these two genera sister-taxa.

Genus	Flagellum of Antenna 2			Pleonal formula	No. articles in Mxp palp	Uropods	
	Multi-articulate	Clavate	Vestigial			Uniramous	Biramous
Barnardidotea Menzies & Miller	X			1 + 0	3	X	
Crabyzos Bate	X			0 + 3	5	X	
Engidotea Barnard	X			1 + 2	5	X	
Glyptidotea Stebbing	X			0 + 3	5	X	
Moplisa Moreira	X			0 + 1	3	X	
Pentias Richardson	X			0 + 3	5	X	
Paridotea Stebbing	X			1 + 2	5	X	
Synidotea Harger	X			0 + 1	3	X	
Synischia Hale	X			0 + 3	5	X	
Idotea Fabricius	X			2 + 1	4–5	X	
Colidotea Richardson	X			0 + 1	4	X	
Synisoma Collinge	X			0 + 0	4	X	
Zenobianopsis Hale	X			2 + 2 4 + 1 ?	5	X	
Euidotea Collinge	X			0 + 3	4	X	
Cleantiella Richardson		X		1 + 2	5	X	
Erichsonella Richardson		X		0 + 0	4	X	
Eusymmerus Richardson		X		0 + 1	4	X	
Parasymmerus Brusca & Wallenstein		X		0 + 1	3	X	
Lyidotea Hale		X		0 + 3	3	X	
Zenobiana Risso (as *Zenobia*)		X	X	3 + 1	5		X
Cleantioides Kensley & Kaufman		X		3 + 1	4–5	X	
Edotea Guerin-Meneville			X	0 + 1	3	X	

of lateral incisions (generally referred to as "suture lines"). Presence of free lateral margins on the fused pleomeres is taken to represent incomplete fusion (i.e., medial fusion only) of these somites, and hence a less derived state than absence of the free lateral margins (i.e., complete fusion).

Maxillipeds.—The palp of the idoteid maxilliped is composed of 5 or fewer articles. Out-group analysis indicates the plesiomorphic state (occurring in all families except Idoteidae) is 5 free articles; reduction in the number of articles thus represents a derived condition. It is not known with certainty whether reduction in the number of articles is due to fusion or to actual loss, although Brusca and Wallerstein (1979*a*) have suggested that both processes may exist among various genera (e.g., loss in *Idotea*, fusion in *Zenobiana*).

Antennae.—In valviferans, the flagellum of the second antenna is either (1) multiarticulate (the primitive condition); (2) reduced to a single clavate article with 1 to 4 minute "vestigial" apical articles; (3) reduced to a single clavate article only; or (4) reduced to just the minute "vestigial" articles. Brusca and Wallerstein (1979*a*) point out that these two kinds of reduction (clavate vs. vestigial articles) are probably the result of two different processes, the former being a case of fusion of the flagellar articles, the latter being an actual loss or reduction in the number of articles, creating a "vestigial" flagellum. In one genus (*Zenobiana*) both the clavate condition and/or the vestigal condition may both occur, suggesting that the two morphologies are somehow linked, perhaps both developmentally and phylogenetically. The early reduction was apparently a situation in which partial fusion of the flagellar articles produced the clavate mor-

phology while retaining a few vestigial, unfused, apical articles (as seen in some *Zenobiana* species). This condition could have progressed in either of two directions—loss of the vestigial articles to leave just the remaining clavate process (as in *Cleantiella, Erichsonella, Euysmmerus, Parasymmerus, Cleantioides,* and *Lyidotea*), or loss of the clavate process to leave just the remaining vestigial articles (*Edotea* and some species of *Zenobiana*). The relationships between the clavate and vestigial conditions may not be resolvable in a phylogenetic sense, and may represent differing avenues of a flexible developmental program. However, unlike the pleonal and maxillipedal palp characteristics (above) which show varying degrees of reduction, the antennal flagella are either reduced (states 2–4 above) or not reduced.

Coxal plates. Although the coxal plates have been used extensively in valviferan taxonomy, use of these structures has not been consistent. Previous workers have treated these structures in a variety of ways and one worker's description is not always comparable to another's. These problems have been discussed at length by Nordenstam (1933), Sheppard (1957), and Brusca and Wallerstein (1979*a*). For these reasons, the coxal plates are not considered in the following analysis.

While the genera of the Idoteidae appear to be reasonably well-defined, the 5 nominate subfamilies are not. The subfamily Idoteinae stands apart from the other 4 in numerous features, and appears to represent a monophyletic group. The other subfamilies (Glyptonotinae, Chaetilinae, Parachiridoteinae, and Mesidoteinae) cannot be easily separated from one another, nor be distinguished unambiguously in a cladogram. For this reason, these 4 subfamilies collectively are herein considered an out-group of the Idoteinae. They may be thought of as representing an unresolved polychotomy on the cladogram in Fig. 4. In the following discussion these 4 subfamilies are treated as one and referred to as the "glyptonotine-group."[4] A second out-group used to construct a cladogram of Idoteinae genera is the Hologнathidae (see Fig. 2). Numbers in the following discussion correspond to that on the cladogram in Fig. 4.

The glyptonotine-group is distinguished by the following synapomorphies: (1) cephalon strongly produced laterally, moving eyes to dorsal position; (2) body broadened and dorsoventrally depressed; (3) pereopods I–III subchelate or prehensile. It retains the symplesiomorphy of separate penes. The Idoteinae is distinguished by the following synapomorphies: (4) reduction of the pleon to the 3+1 condition; (5) fusion of the penes into a single structure (Fig. 4).

Paleontological data, limited as they are, corroborate the out-group comparison for the Idoteinae. The oldest known idoteid fossils are referred to the monotypic genus *Proidotea* (*P. haugi* Racovitza and Sevastos, 1910), from mid- to late Oligocene deposits of eastern Europe. This genus clearly falls within the subfamily Mesidoteinae (the glyptonotine-group). The only other fossil data for the Valvifera are Pleistocene to Recent specimens of *Saduria* (=*Mesidotea*)—probably the holarctic *S. sabini* (Krøyer). In both of these genera, the pleon is composed of 4 somites, plus the pleotelson. The maxillipedal palp of *Saduria* is 5-articulate. The uropods of Mesidoteinae are biramous, as in the subfamilies Glyptonotinae, Chaetilinae, and Parachiridoteinae.

The genus *Zenobianopsis* Hale, 1946 is not indicated on the cladogram (Fig. 4). The status of this deep water taxon is uncertain. Only two species have been reported and they differ markedly in morphology. Species of *Zenobianopsis* have a pleon of 4 free somites, plus indications of a fifth (although in *Z. caeca* Hale, 1946, these somites appear somewhat reduced). Other attributes indicate that *Zenobianopsis* is a very primitive member of Idoteidae (Table 1), presumably with its origin at or about the time of separation of the Idoteinae from the glyptonotine-group. The early isolation of these species is further suggested by the fact that both are known only from deep subantarctic waters of the Indian Ocean. *Zenobianopsis* is indicated by a dashed line in the evolutionary tree in Fig. 16; further research may place the two species in separate genera.

Within each of the two principal idoteine lineages depicted in Fig. 4, the trend towards fusion of pleomeres is expressed in a "directed" fashion. That is, the greater the degree of pleomere fusion in a taxon, the farther up the cladogram it appears. Fig.

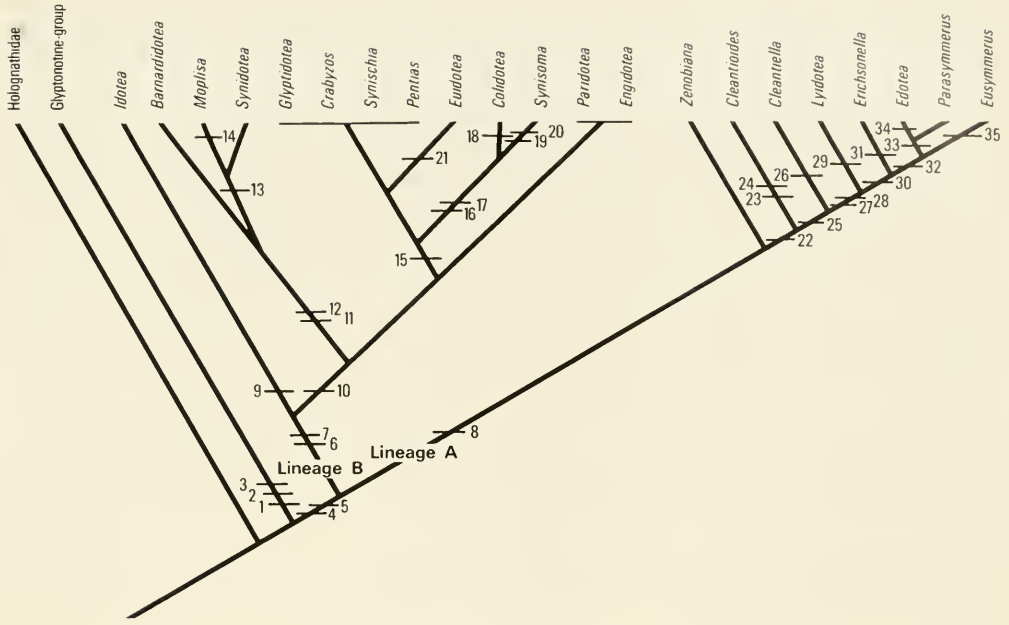


FIGURE 4. Cladogram of Idoteinae genera. Only apomorphies are indicated. Numbering of characters corresponds to discussion in text. For characters uniting Holognathidae to Idoteidae *see* Fig. 2 and text.

3 provides a schematic representation of known pleonal morphologies beginning with the 4-segmented pleon found in the glyptonotine-group. The pleonal formulas are written in two digits, separated by a plus sign. The first digit is the number of complete pleomeres present in the pleon (not counting the pleotelson); the second digit is the number of lateral incisions present, representing remnants of incompletely fused pleomeres.

There are 14 possible combinations or pleonal formulas that species of Idoteinae might possess: 3+1, 3+0, 2+2, 2+1, 2+0, 1+3, 1+2, 1+1, 1+0, 0+4, 0+3, 0+2, 0+1, 0+0. However, there are over 100 possible different steps in which fusion may progress to give rise to these 14 combinations. Each of these 100+ pleonal morphologies is derived in a unique manner and hence each constitutes an "attribute" (*sensu* Platnick, 1979:542). Not every pathway is represented in Fig. 3; only enough steps are shown in order to reach the existing morphologies of the known idoteine genera in a parsimonious fashion. This large "uncertainty" problem, as well as the seeming parallelism of pleonal fusion, can be resolved by careful examination of the schematic pattern analysis in Fig. 3. All known genera of Idoteinae have pleonal formulas that must have arisen from one of two main lines; one line beginning with a 3+1 configuration (indicated on Figs. 3 and 4 as "lineage A"), and the other beginning with a 2+1 configuration (indicated on Figs. 3 and 4 as "lineage B"). Assignment of genera to one or the other of these lineages can be based on the antennal features described above. That is, the 13 genera with multiarticulate second antennal flagella are hypothesized to represent a lineage or series distinct from the 8 genera that have lost the multiarticulate conditions. Any other assignment of these genera requires accepting convergent evolution of these antennal morphologies; parsimony is maintained by presuming these antennal morphologies to have arisen only once. This split clearly places all genera on one or the other of these two main lines of descent involving pleomere fusion, and further suggests that evolution of identical pleonal formulas in these two lines of descent was through different steps, and hence not true convergence at all.

Not all 14 possible patterns are represented by extant species. In fact, only 9 are known at present (4+1, 3+1, 2+1, 2+2, 1+2, 1+0, 0+3, 0+1, 0+0). Other morphologies

presumably existed in the past (in extinct intermediate taxa) or exist at present but await discovery. Fig. 3 predicts the nature (overall morphology) of these yet to be discovered genera, and hence sets the stage for testing the hypotheses contained therein.

Fig. 3 is not a cladogram OR an evolutionary tree. It is merely a graphic arrangement of pleonal morphologies in a sequence of most primitive at the top, with increasingly derived morphologies (increased fusion) expressed following the arrows down and across. As can be seen in Figs. 3 and 4, reduction in pleomere number corroborates the reduction in the antennal flagellum (i.e., there are no conflicts).

Lineage B (Fig. 4) is distinguished by two synapomorphies: (6) pleonal fusion has advanced to the 2+1 morphology, and (7) the uropods have lost the primitive biramous morphology, deriving a uniramous condition. Lineage A is defined by the synapomorphy of (8) antennal flagellum reduction to condition 2 described above (i.e., fusion of most flagellar articles into a clavate process bearing on its apex a few remaining "vestigal" articles).

Within lineage B, the genus *Idotea* is distinguished by the apomorphy of (9) reduction in maxillipedal palp article number; the sister-group to *Idotea* has reduction of pleonal morphology beyond the 2+1/2+0 condition (10). *Barnardidotea, Moplisa,* and *Synidotea* have maxillipedal palp reduction to 3 articles (11), as well as continued fusion of pleomeres to produce a 1+0 pleonal morphology (12). *Barnardidotea* is distinguished from *Moplisa* and *Synidotea* by retention of the 1+0 pleonal formula, while the latter two genera have achieved the 0+1 condition (13). *Moplisa* and *Synidotea* can be distinguished from one another by the loss of the molar process in the former (14).

The *Paridotea-Engidotea* line is distinguished from its sister-group by retention of the symplesiomorphic pleonal condition, 1+2 (vs. the synapomorphic condition, 0+3) (15). These two genera cannot be clearly distinguished from one another on morphological criteria as they are currently understood. The *Colidotea-Synisoma* group is distinguished from its sister-group by two synapomorphies: (16) lacinia mobilis of mandible greatly enlarged (as large or larger than incisor process), and (17) reduction to a 4-jointed maxillipedal palp. *Colidotea* is distinguished by (18) a 0+1 pleonal morphology. *Synisoma* is distinguished by two synapomorphies: (19) pleonal morphology 0+0, and (20) an elongate pleon (⅓ or more total body length). *Euidotea* is distinguished from its sister-group by (21) possession of a 4-jointed maxillipedal palp (vs. 5-jointed in the *Glyptidotea-Pentias-Crabyzos-Synischia* line). The latter 4 genera cannot be distinguished by morphological criteria as they are currently understood and are hereafter referred to as the *Glyptidotea*-group.

Within lineage A, *Zenobiana* can be distinguished only by the symplesiomorphous retention of biramous uropods; whereas its sister-group has achieved the synapomorphic condition of uniramous uropods (22). Some species of *Zenobiana* have lost the minute apical articles on the tip of the second antennae, while others retain these terminal articles. I am in agreement with previous authors that these differences do not warrant the splitting of *Zenobiana* into several genera (e.g., Bate and Westwood 1861–1868, Issel 1913, Collinge 1917, Barnard 1925). I have not taken the presence or absence of the "vestigial" articles into consideration in construction of the cladogram.

Cleantioides, as defined here, contains only two species, *C. occidentalis* (Richardson) and *C. planicauda* (Benedict). This genus is distinguished by 2 synapomorphies: (23) reduction of the fourth pair of pereopods to nonambulatory appendages, and (24) reduction of the maxillipedal palp to 4 articles in one species (*C. occidentalis*). It retains the symplesiomorphic 3+1 pleonal morphology, while its sister-group has achieved the 2+2 or less stage (25).

Cleantiella is distinguished by the apomorphy of pleonal reduction to the 1+2 condition (26). *Lyidotea* and its sister-group bear 2 synapomorphies: (27) the pleon has achieved the 0+3 morphology, and (28) the maxillipedal palp has been reduced to the 3- or 4-articulate condition. *Lyidotea* bears an apomorphic condition in which the last pereonal somite has become fused with pleomere 1 (29); its sister-group is distinguished by the 0+2 or less pleonal morphology (30).

Erichsonella is distinguished by the apomorphy of (31) complete pleonal fusion, resulting in the 0+0 condition, although some species retain a faint transverse furrow presumably representing the fused juncture of pleomere 1 to the remainder of the pleon. *Erichsonella*'s sister-group (*Eusymmerus-Parasymmerus-Edotea*) has achieved the 0+1 morphology (32). *Edotea-Parasymmerus* are defined by the synapomorphy of maxillipedal palp reduction, to the 3-articulate condition (33). *Edotea* is distinguished by its acute subtriangular pleon (34). *Eusymmerus* is distinguished by the unique 3-pointed spine that arises between the lacinia and incisor process on the left mandible (35).

This cladogram (Fig. 4) reduces the number of character convergences to two. Reduction in the number of articles on the maxillipedal palp appears to take place time and again, throughout the various idoteine lines, and no sensible cladogram design can eliminate it. In Fig. 4 it occurs four times in lineage A and three times in lineage B. For this reason, it was given lower priority than all other characters used in the analysis. Maxillipedal palp reduction is common throughout the order Isopoda and represents a kind of convergence or parallelism known as canalized evolutionary potential. This character also expresses both "inside" and "outside" parallelism (*sensu* Brundin 1976, 1981). The second convergence (or parallelism) is loss of the ancestral biramous uropod condition, which takes place in (and characterizes) lineage B, and then again in the *Cleantioides* through *Eusymmerus* line of lineage A (synapomorphy 22).

While the cladogram in Fig. 4 is highly parsimonious, what is clearly needed is the elucidation of additional synapomorphies to further test the contained hypotheses. Six terminal taxa (or groups) cannot be distinguished by unique apomorphies at this time. As Sheppard (1957) and Brusca and Wallerstein (1979*a*) pointed out, a critical examination of the nature of the pereopodal coxae in the various idoteid genera will surely prove enlightening and undoubtedly provide us with a new suite of character states with which to test evolutionary relationships among the genera. The exact nature of the reduction in flagellar articles on the second antennae needs to be investigated (particularly regarding *Zenobiana, Cleantioides,* and *Edotea*), and this too might shed new light on the cladogram. This reduction, as well as reduction in maxillipedal palp articles and free pleomeres, tends to follow Brown's (1965) "Rule of Evolutionary Reduction." Finally, two unresolved polychotomies exist within the Idoteinae that can be resolved only by synonymizing genera or by the elucidation of new characters to differentiate these taxa. It is my belief that a careful study of the coxal plates, lacinia mobili, second antennae, and pleopods 3–5 could resolve all of these problematic areas among the idoteine genera.

Biogeography and Evolution of the Idoteinae Genera

Idoteids, like other isopods, brood their developing young in a marsupium, from which they are hatched as "mancas," which are subjuveniles that resemble miniature adults except for lacking the seventh pair of pereopods. There is no evidence, ecological or morphological, that the manca stage is planktonic, and in those species that have been reared in the laboratory, hatchlings are always benthic crawlers like their parents. The only published records of idoteids in plankton are for the 2 widespread species, *Cleantioides planicauda* and *Idotea metallica,* and the 2 species belonging to the questionable genus *Zenobianopsis.* Both mancas and adults of most species, however, are capable of swimming in short bursts over small distances (e.g., between algal fronds). When idoteids are dislodged from the substratum by waves or surge they sink or swim quickly to the bottom (Jansson and Matthiesen 1971, Salemaa 1979, Sywula 1964, Lee and Gilchrist 1972, Wallerstein and Brusca 1982). Idoteids are clearly a component of the benthic community in marine shallow-water habitats, where their niche is that of a cryptic herbivore and occasional scavenger. This suggests that idoteids, particularly intertidal species, are probably not good dispersers.

Because the following discussion deals with the Idoteinae at the generic level, it must remain fairly general. Even at this level, however, these generalizations describe patterns of geographic distribution that can be correlated with the cladogram (Fig. 4),

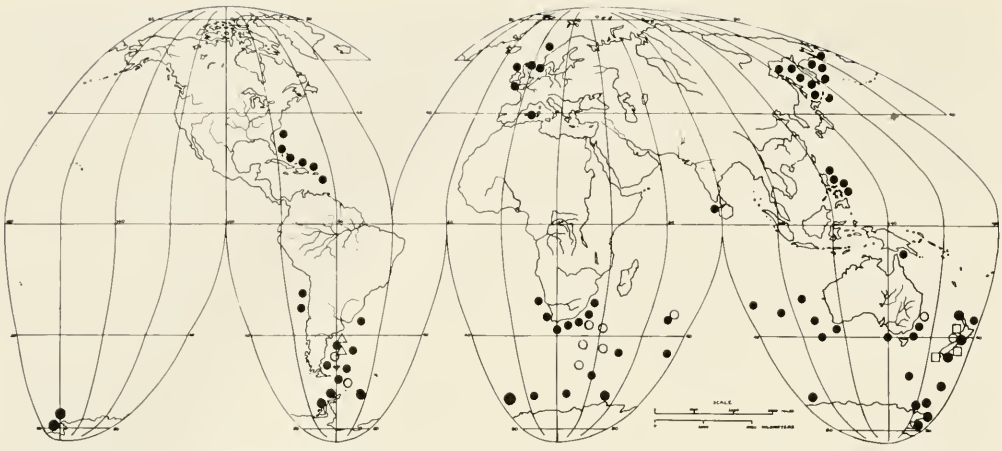


FIGURE 5. Distribution of valviferan families (excluding Idoteidae): Amesopodidae [o], Arcturidae [●], Holognathidae [□], Pseudidotheidae [O], Xenarcturidae [△].

and which can most parsimoniously be ascribed either to vicariance or non-vicariance events. Geological dates of events described in this section have been used to transform the cladogram into the evolutionary tree depicted in Fig. 16. It is not my purpose to present a detailed analysis of each genus here; that must await a species-by-species study of each genus (e.g., see Brusca 1983 for the genus *Colidotea*). The latter will clearly be an enormous undertaking, but one for which the following analysis could provide a starting point.

The Valvifera as a whole show strong correlation to southern temperate latitudes, 3 of the 6 families being restricted to that geographic region, 1 known only from the shores of India, and the other 2 being widespread (Fig. 5). The idoteine genera show a similar geographic trend (Figs. 7–14). Numerous studies have recently appeared that examine the relationships of distributional patterns of terrestrial flora and fauna to the geological history of the Southern Hemisphere (e.g., Keast 1973, Raven and Axelrod 1972, Cracraft 1974, 1980). However, similar studies on marine groups have been few. For these reasons, Gondwanan shores are discussed in some detail. A brief review of the breakup of Gondwana follows, based on Kennett (1977), Smith and Briden (1977), Norton and Sclater (1979), Knox (1979), Durham (1979), Grant-Mackie (1979) and Hallam (1981).

Throughout most of the Permian, the Triassic, and most of the Jurassic periods, Gondwana was unified as a single land mass. The proto-southern continents were all situated at higher latitudes than they are today. Although Permian glaciation probably existed in the highest southern latitudes, that cold era came to a fairly abrupt halt by the Jurassic. By mid-Mesozoic times climates in the Southern Hemisphere had changed markedly, as a long-lasting global warming trend became established. Paleontological evidence suggests that by the middle or late Jurassic the northern shores of Gondwana had already begun acquiring a warm-water Tethyian biota, thus restricting temperate coastal biota to the southernmost latitudes. A common temperate marine fauna probably inhabited the contiguous coastline of Gondwana south of 55°–65°S latitude. This shallow coastal sea washed the shores of southernmost South America, southeast Africa, eastern Antarctica and eastern Australia. The continuous coastal topography, coupled with non-glacial and generally equable climates of the Jurassic, facilitated "warm-water cosmopolitanism" along the shores of northern Gondwana, and "cold-water cosmopolitanism" along the shores of southern Gondwana. These two regions were probably physically isolated from one another until at least the early Tertiary, when separation of Australia from Antarctica instituted a direct high latitude southern connection between the Indian and Pacific oceans. The distribution of modern coastal temperate

faunas in the Southern Hemisphere can thus be hypothesized to be, at least in part, the product of the fragmentation of an early to mid-Mesozoic temperate Gondwanan track.

That part of Gondwana composed of Antarctica, Australia, New Zealand and South America rotated southward during the Mesozoic, although as early as the Late Jurassic these land masses were beginning to separate as Antarctica-Australia-India began uncoupling from Africa and South America. By the Early Cretaceous (about 120 MYA) sea floor spreading had started to form the south Atlantic Ocean. At about the same time, India began to decouple from Antarctica-Australia-Africa. Marine conditions developed between India and Antarctica-Australia by 105 MYA. Africa was clearly separated from Gondwana about 90 MYA. New Zealand split from Antarctica-Australia 70–80 MYA. By the mid-Cretaceous the south Atlantic Ocean was open along its entire length as Africa and South America pulled away from one another. The free ocean connection (the "Vema Gap") between the north and south Atlantic was established by the Late Cretaceous as the transverse Rio Grande-Walvis Ridge sank below the 1 km depth (approximately 78–80 MYA). Australia was last to decouple from Antarctica, about 50–60 MYA. During the Paleocene these land masses were probably separated by a shallow narrow seaway; however, the South Tasman Rise acted as an effective barrier to the development of a circum-Antarctic current until about 30–50 MYA, subsequent to which the southern circum-polar current began to develop. The modern deep-flowing Antarctic Circumpolar Current could not have been established until the opening of the Drake Passage, 22–28 MYA, when deep-sea conditions developed between southern South America and Antarctica (plate boundaries and timing of geotectonic events in this region are still very controversial).

During most of the course of events described above, Antarctica continued a slow drift southwards, reaching a position close to its present location by Late Cretaceous; it has remained nearly stationary throughout the Cenozoic. Thus, deep marine conditions began to develop in the Southern Ocean by the Late Paleocene, although a corridor of scattered highlands and shallow seas persisted between Australia and Antarctica until about the Late Eocene or Early Oligocene.

South America has moved progressively westward since the Late Cretaceous. India collided with Asia about this same time. Coincidental with this southern fragmentation, the highest post-Carboniferous sea levels ever to occur (Campanion Era, about 75 MYA) submerged roughly ⅓ of the present continental area below shallow epicontinental seas. Deep water flows from the Pacific into the Atlantic across Central America commenced about 55 MYA, only to be halted in the Pliocene when the Panama Isthmus emerged.

The shallow-water marine fauna would not have responded to the breakup of Gondwana in the same manner as the terrestrial fauna, because the initial separation of the land masses created intervening shallow seaways that fostered the spread of marine biota before separation of the biotas occurred (for a comparison with the fragmentation of the terrestrial fauna of Gondwana see Cracraft 1974 and Rosen 1978). As South America and Africa moved northward, and Antarctica moved southward, relative to one another, the effect on temperate coastal marine life was most likely to have created two disjunct faunas. One of these faunas, the western coastal fauna, would have inhabited the shores of southern South America, southern Africa, and northwestern Antarctica. The eastern fauna would have been restricted to Australia, eastern Antarctica and southernmost India. New Zealand, at this time, was situated in warm-water latitudes. By the mid-Cretaceous, the Southern Ocean had become extensive enough to break the western fauna into two separate temperate regions: southern South America (and probably the region of the Antarctic Peninsula) and southern Africa. The eastern Gondwana, mid-Cretaceous, temperate coastal region remained unchanged even though New Zealand had split from the warm-water shores of Australia. By the mid- to Late Cretaceous the shallow sea between India and Antarctica had deepened to isolate these regions entirely from one another, India having drifted into the tropical waters of the Indian Ocean. The coastal environment of southern Australia remained

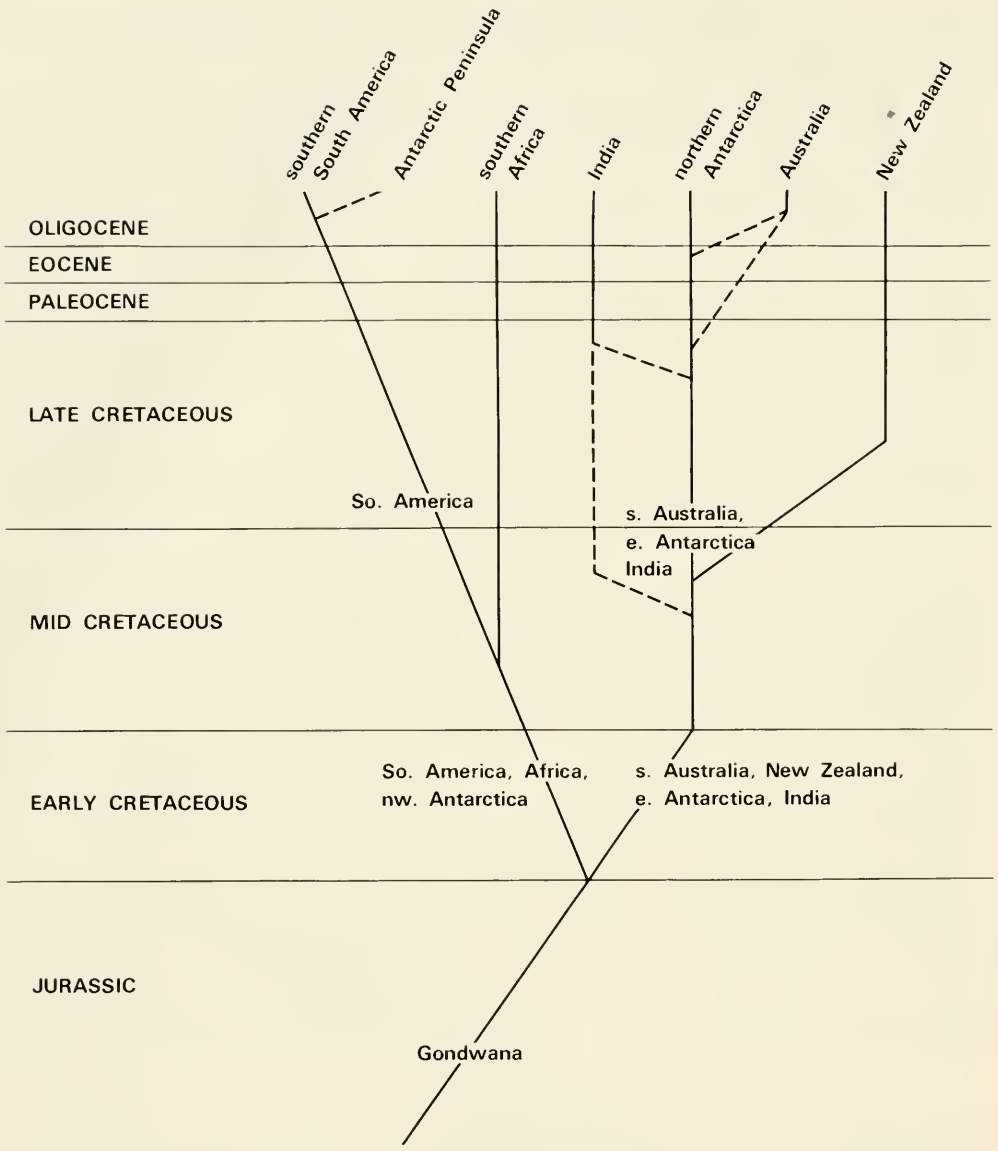


FIGURE 6. Proposed geographic cladogram of temperate, shallow-water, Gondwanan coastal areas. Note the significant differences between this cladogram of shallow continental shores (marine geographic areas) and Rosen's (1978) cladogram of Gondwanan continents (terrestrial geographic areas). *See* text for discussion.

tied to northern Antarctica until the Cretaceous-Tertiary boundary, or perhaps even to the Early Oligocene. These relationships are pictured in Fig. 6.

Because paleoclimates and oceanographic conditions were not the same during the Mesozoic and Cenozoic as they are today, latitudinal distributions of shallow-water marine life would have been under quite different thermal regimes. This ecological component must be taken into account when considering paleobiogeographical reconstructions. A brief review of Mesozoic-Cenozoic climates follows; for more detailed information consult Fleming (1975, 1979), Margolis et al. (1978), Grant-Mackie (1979), Durham (1979), Frakes (1979), Zinsmeister (1982), and references therein.

Overall, middle and late Mesozoic climates were extremely equable, with ocean temperatures exceeding those of the present day by 7°–15°C. Polar ice caps did not

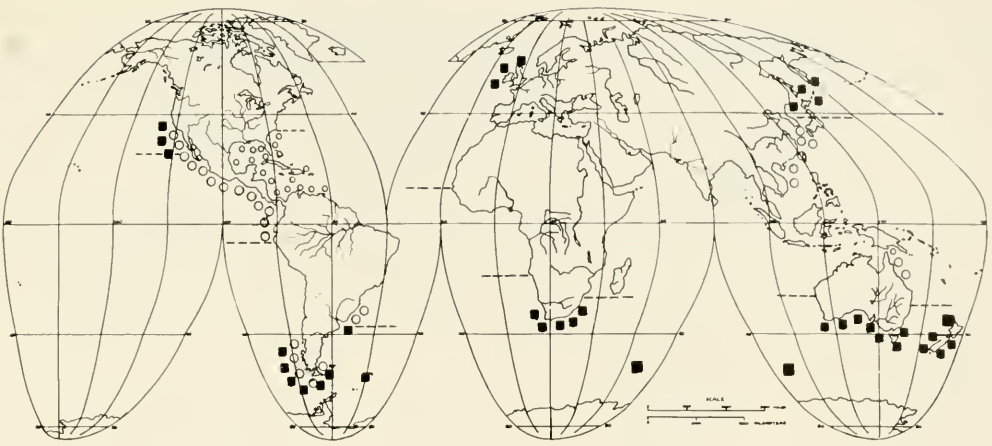


FIGURE 7. Composite distribution map of all idoteine genera, except the 3 cosmopolitan taxa (*Idotea, Synidotea, Zenobiana*). Dashed lines indicate limits of warm-water (tropical/subtropical) regions; open circles = genera of lineage A; closed boxes = genera of lineage B.

exist and both terrestrial and marine biotas exhibited little evidence of latitudinal zonation. Cosmopolitanism was common. Cool sea water existed in the southern oceans only south of about 50°S latitude. Early Cretaceous sea bottom temperatures were approximately 10°–15°C warmer than today; Late Cretaceous sea bottom temperatures were approximately 7°C warmer than today. The Eocene marked the beginning of a global cooling trend that ultimately led to the Cenozoic glaciations and cooling of deep ocean bottom waters to their present thermal regimes (Shackleton and Kennett 1975). As late as the Eocene (38–55 MYA), all but the southernmost Antarctic seas were warm-temperate in nature. The steep thermal drop over the Eocene/Oligocene boundary was probably related to the establishment of the Antarctic Circumpolar Current and subsequent South Polar glaciation. Although land masses occupied both poles by the Early Paleocene, large-scale Antarctic glaciations probably did not begin until the Miocene. The Antarctic Convergence began moving northward in the Oligocene. Cooling trends continued throughout the Cenozoic, apparently marked by several periods of severe chilling.

Fossil reefs, requiring relatively warm surface waters, grew to paleolatitudes of about 40° throughout the Paleogene, as in the Cretaceous. In the northeast Pacific, tropical environments (i.e., surface temperatures $\geq$20°C) extended to approximately 45°N in the Eocene, and have contracted equatorward steadily since that time. Abundant paleoceanographic and stratigraphic data exist to indicate that New Zealand shores were bathed primarily by warm subtropical waters throughout the Cretaceous and Paleocene (Fleming 1962, 1975, Durham 1979, Knox 1979), although a distinct cooling trend began in the middle to Late Miocene, eventually resulting in present-day temperate coastal conditions. At best, only southernmost New Zealand might have experienced temperate waters from the Eocene to the Miocene. By early Pleistocene subantarctic waters had reached about 40°S latitude on New Zealand shores. The middle Oligocene marked the end of "high latitude subtropical communities," and by the Late Miocene modern water bodies and their associated biological provinces had begun to be established. The Australian Subantarctic water mass had formed by about 15 MYA. For the past 10–15 million years the Southern Ocean temperature, circulation and zonational water masses have remained essentially the same.

If the distributions for all species of Idoteinae are plotted on the globe, nearly every sea and shore is seen to be inhabited by one or more genera. Fig. 7 is a composite distribution map plotting the ranges of all taxa of Idoteinae EXCEPT the 3 cosmopolitan genera—*Idotea, Synidotea,* and *Zenobiana.* These 3 taxa are omitted from the com-

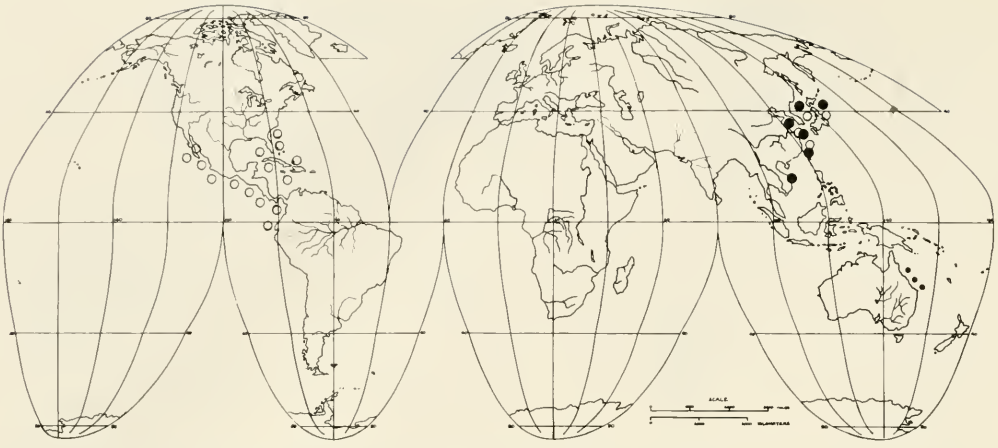


FIGURE 8. Distributions of *Cleantiella* [●], *Lyidotea* [•], and *Cleantioides* [○].

posite distribution map because they provide no particular insights into a global pattern analysis at this level. Distribution maps of the individual genera are given in Figs. 8–14, and are discussed below. It will be seen from these distribution maps and the following discussion that most idoteine genera are endemic to only one or a few coastal regions. The dashed lines on Fig. 7 indicate the limits of the tropical/subtropical regions, based on Ekman (1953), Briggs (1974), and Brusca and Wallerstein (1979*b*). While some disagreement exists regarding the exact limits of the tropical zones, the latitudes that I have chosen clearly separate the "warm-water" faunal regions of the world's shores from the "cold-water" regions. The only serious arguments with these delimitations might be in whether one regards the Mediterranean Sea as warm-temperate or subtropical. The best comprehensive discussion of Mediterranean zoogeography is probably that of Ekman (1953), who in describing the complex mixtures of northern and southern elements, couldn't comfortably label this sea either warm-temperate or subtropical. The nature of south African faunal designations has also been a matter of some controversy, and was recently reviewed by Brown and Jarman (1978).

Several general patterns are revealed when Fig. 7 is examined. In the New World, endemic idoteine genera are distributed fairly equally in both warm and cold waters. In the Old World, however, there is a marked absence of records from the tropics. Only 3 genera on this map represent Old World tropical taxa: *Cleantiella* and *Cleantioides* both occur on the east Asian coast, while *Lyidotea* is known from a single species in northeastern Australia (see Fig. 8). A second pattern seen is that Old World endemic genera tend to form 3 distinct clusters, as follows: (1) a Southern Hemisphere cold-water group, (2) a European cool- to cold-water group, and (3) a northeast Asian cool- to warm-water group. Only 2 of the genera depicted in Fig. 7 occur in both the Old and New Worlds: the southern temperate *Paridotea* and the northern tropical *Cleantioides*. Because most species and genera of Idoteidae are restricted to temperate or polar seas, the family has long been considered a "cold-water centered taxon" (see Brusca and Wallerstein, 1979*b* and references therein). It is of particular interest that the Old World and New World tropical regions are inhabited by entirely different genera. The New World tropical genera are *Cleantioides, Erichsonella, Parasymmerus,* and *Eusymmerus*. The Old World tropical genera are *Cleantiella, Lyidotea, Idotea, Synidotea,* and *Zenobiana*. As the latter 3 are largely cosmopolitan taxa, the obvious question is, "Why have species in these genera been unable to invade the tropics in the New World?" Let us now examine the distributions of the individual idoteine genera.

Idotea is nearly a cosmopolitan genus (Fig. 9). It occurs in most waters of the Old World, including the tropics, but in the New World it is notably absent from the warm seas between the Tropics of Cancer and Capricorn in both the Pacific and Atlantic.

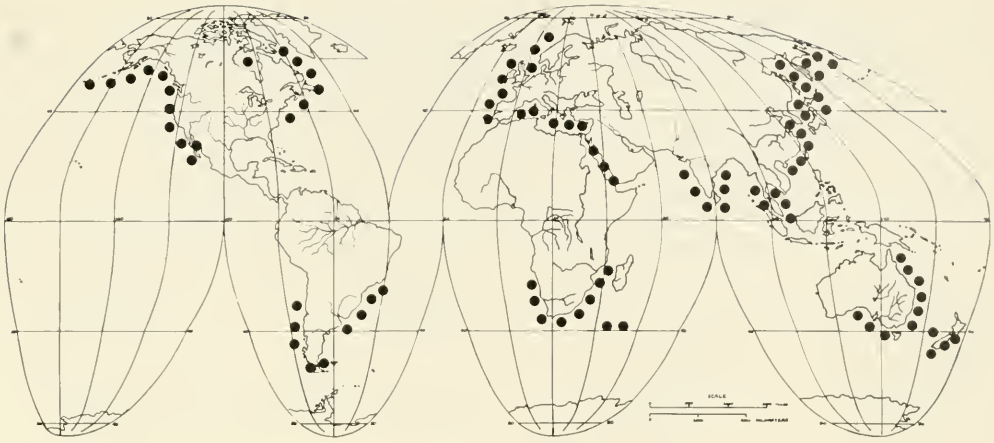


FIGURE 9. Distribution of *Idotea*.

Brusca and Wallerstein (1979*b*) reviewed literature documenting the eurythermal nature of *Idotea* species, and suggested that biological factors (competition or predation), rather than temperature, could be excluding the 2 New World temperate isopod genera, *Idotea* and *Synidotea*, from the Western Hemisphere tropics. Wallerstein and Brusca (1982) subsequently provided experimental and comparative morphological evidence that predation by crustacivorous fishes is possibly restricting species of *Idotea* from the New World tropics. In the latter study they proposed a model that envisioned "faunal waves" of tropical predator species (primarily fishes) moving northward from the equatorial region during warm Pleistocene interglacials, pushing the southern latitudinal range end points of non-adaptable temperate species northward ahead of them, and thus excluding *Idotea* and *Synidotea* from the New World equatorial region (see Addicott 1970 and Zinsmeister 1974 for a discussion of similar north-south faunal displacements in Mollusca). The nearly global distribution of *Idotea*, as well as its position on the cladogram (Fig. 4) relative to other genera in lineage B (see discussion below) suggests that *Idotea* is an old genus (pre-Cretaceous). It should be emphasized that, while the genus *Idotea* is cosmopolitan, the species in this taxon are themselves largely endemic to restricted coastlines. Only one species of *Idotea* is cosmopolitan, *I. metallica*. Its cosmopolitanism has been explained by drift dispersal of the algae on which it lives (Naylor 1972, Poore 1981).

Nine of the 12 remaining genera in lineage B are endemic to the Southern Hemisphere (Table 2) and are probably descendants of a pan-austral, cold-water, Gondwanan, pre-Cretaceous fauna. The concept of a pan-austral terrestrial biota was apparently first recognized by Hooker (1853, 1860) and Huxley (1868). Though largely suppressed by 100 years of "Wallaceian dispersalism," the concept has finally experienced a rebirth owing largely to the work of Pantin et al. (1960) and Brundin (1966, 1970, 1972*a*, *b*, 1976). For a recent summary of many subsequent papers see N.Z. DSIR (1979). Only recently, however, has serious documentation and discussion of generalized temperate pan-austral marine tracks begun (e.g., Zinsmeister 1976, 1982, Fleming 1975, Knox 1975). The mid-Cretaceous/early Tertiary fauna that inhabited this temperate, shallow-

TABLE 2. Distribution of the 8 Idoteinae Genera of Lineage B Endemic to the Southern Hemisphere.

Geographic occurrence	*Moplisa*	*Paridotea*	*Euidotea*	*Crabyzos*	*Synischia*	*Glyptidotea*	*Barnardidotea*	*Engidotea*
Southern South America	+	+						
South Africa		+	+			+	+	+
Southern Australia		+	+	+	+			
New Zealand		+	+	+				

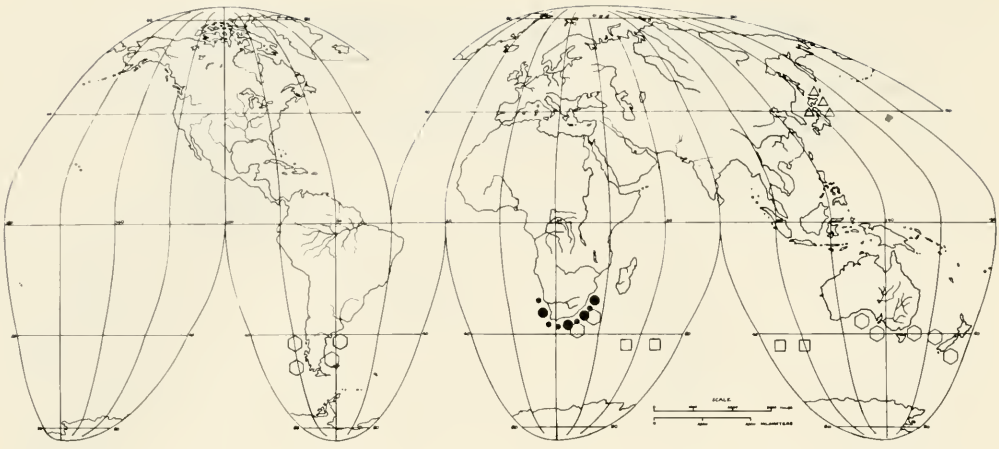


FIGURE 10. Distributions of *Glyptidotea* and *Barnardidotea* [●], *Engidotea* [•], *Pentias* [△], *Zenobianopsis* [□], and *Paridotea* [○].

water, southern Gondwanan region has been referred to as the Weddellian Province by Zinsmeister (1976).

One of the earliest appearing genera in this post-*Idotea* radiation was *Synidotea*, which like *Idotea* is nearly cosmopolitan but notably absent from the New World tropics (Fig. 11). The same comments that apply to Idotea above are probably applicable to *Synidotea*. The origins of *Synidotea* appear old enough that the Early Cretaceous circum-Arctic seaway probably served as one of several principal dispersal routes, this being reflected in the modern distribution of the genus, which has by far the majority of its species concentrated in the Northern Hemisphere. This hypothesized age of origin, plus the restriction of both *Barnardidotea* and *Moplisa* (*Synidotea*'s sister-group) to the Southern Hemisphere, argues strongly for the origin of *Synidotea* in the southern seas. This contrasts with the opinion of Gurjanova (1935) and Menzies and Miller (1972), who suggested that the place of origin of *Synidotea* was the north Pacific. Menzies and Miller's opinion appears to have been based solely on the fact that most species of *Synidotea* presently occur in this area, which they considered to be its "center of origin." The present analysis, however, does corroborate Menzies and Miller's (op. cit.) dating of the origin of this genus. *Synidotea*'s sister-group, *Moplisa*, consists of a

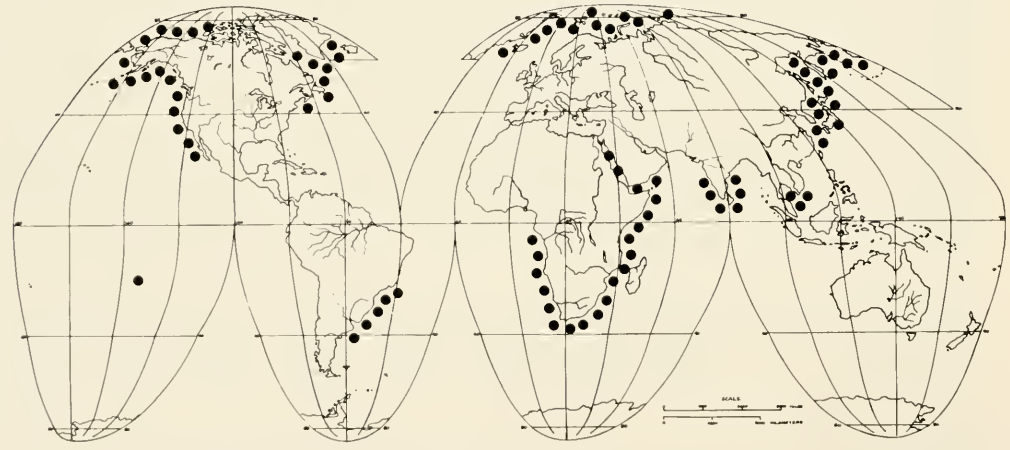


FIGURE 11. Distribution of *Synidotea*.

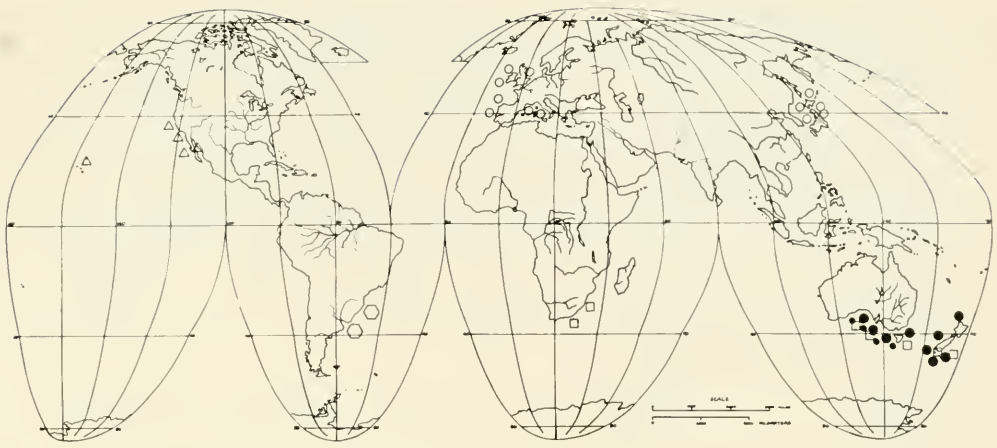


FIGURE 12. Distribution of *Crabyzos* [●], *Synischia* [•], *Euidotea* [□], *Synisoma* [○], *Colidotea* [△], and *Moplisa* [○].

single species, *M. sphaeromiformis* (Mane-Garzon, 1946), so far known only from a short stretch of coastline in southern Brazil (Fig. 12). The cosmopolitanism of *Synidotea* (vs. the restricted distribution of the monotypic *Moplisa*), and the absence of an apomorphy to distinguish *Synidotea* from *Moplisa* strongly suggests that *Moplisa* evolved either in sympatry or as a peripheral isolate from a continuing stock of *Synidotea*. These relationships are pictured in the phylogram (Fig. 16) and are consistent with the cladogram.

Although *Glyptidotea, Crabyzos, Pentias,* and *Synischia* cannot be separated by cladistic analysis (Fig. 3), the biogeographic data provide evidence regarding their origins. *Glyptidotea* is endemic to temperate South Africa (Fig. 10); *Crabyzos* and *Synischia* are endemic to temperate Australasia (Fig. 12). These patterns suggest that these 3 genera arose subsequent to the initial east-west split of Gondwana (i.e., post-Jurassic). The absence of *Glyptidotea* from the South American component of the west Gondwanan track suggests that this genus arose subsequent to the separation of these two land masses (i.e., mid-Cretaceous or later). The closely related genus *Pentias* is today restricted to temperate shores of northern Japan (Fig. 10). The simplest explanation for its occurrence would seem to be fortuitous jump dispersal across the warm

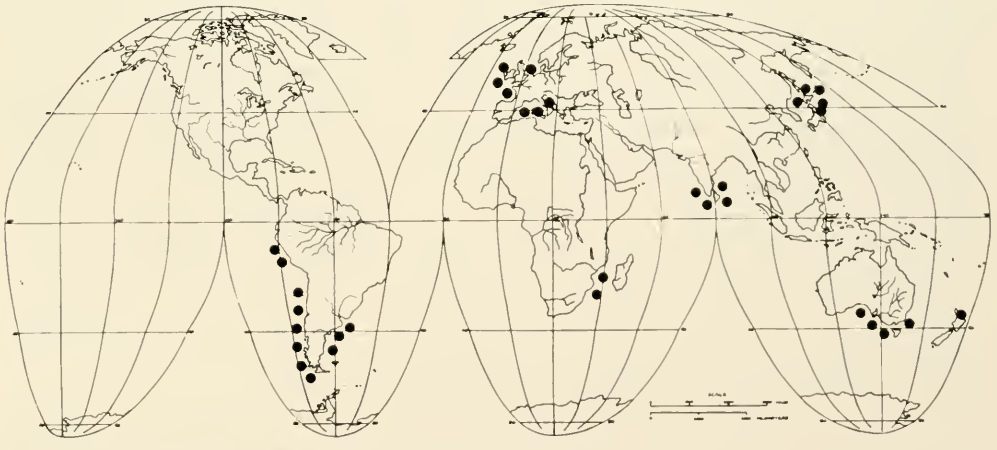


FIGURE 13. Distribution of *Zenobiana*.

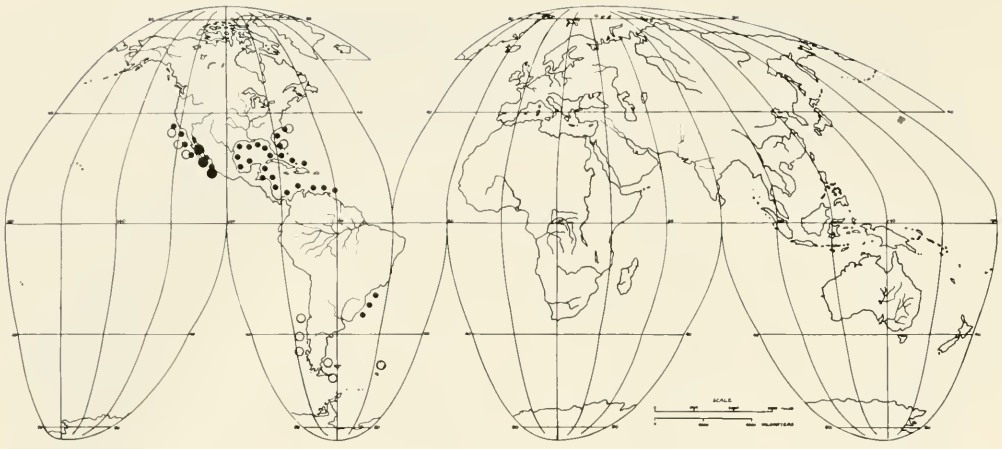


FIGURE 14. Distribution of *Eusymmerus* and *Parasymmerus* [●], *Edotea* [○], and *Erichsonella* [•].

waters of the equatorial region, perhaps during a period of global cooling and tropical compression such as the late Tertiary (although the western Pacific was probably far less affected by marine cooling than other regions on the globe). A second, remote possibility is that it (or its ancestors) reached Japan via China, which may have originally been part of the Gondwanan continent (see Crawford 1974).

None of the above southern taxa occur along the warmer shores of the Indian Ocean. Their distributions suggest that these genera are Cretaceous to post-Cretaceous descendants of the widespread Jurassic-Early Cretaceous temperate Gondwanan track discussed earlier in this section. The ancestor(s) inhabiting this track is indicated in the evolutionary tree by "GonAnc" (Fig. 16).

Because several genera cannot be clearly distinguished from one another by the cladogram, it is difficult to seek congruence between lineage B and the geographic cladogram of Fig. 6. However, a partial correlation (38%) is nonetheless evident (Fig. 15*a, b*). Table 2 provides a distributional summary of the 8 Idoteinae genera of lineage B that are Southern Hemisphere endemics. Fig. 15 gives reduced taxon-area and geographic cladograms for the groups in question. The cladogram congruence with the *Synidotea-Barnardidotea-Moplisa* line corroborates the hypothesis that the latter two taxa arose subsequent to the splitting of South America from Africa, while *Synidotea* continued to persist unchanged. Correlation also exists for *Synischia*. If one accepts the probable dispersal of *Crabyzos* from Australia to New Zealand, the correlation between these cladograms is raised to 50%. *Paridotea* has retained its circumpolar distribution, corroborating its early (pre-Cretaceous) origin.

The occurrence of *Euidotea* on African, Australian, and New Zealand shores (Fig. 12), and its absence from South American coasts today, argues for either (1) its origin prior to the break-off of Africa and its subsequent extinction in South America, or (2) its origin on African shores after the break-off of that continent and its subsequent spread to Australasia via West Wind Drift. Recall that New Zealand probably did not achieve its present temperate coastal thermal regime until well after the deep water barriers were formed that isolated it from Australia, probably not until the Eocene at the earliest. Thus, introduction of the cold-water genus *Crabyzos* could have been via dispersal from Australia in fairly recent times (mid- to late Tertiary). This same reasoning must apply to the other temperate New Zealand genera, *Paridotea* and *Euidotea*. The fact that none of these three taxa are endemic to New Zealand (all 3 also occur in southern Australia) lends support to this probability.

The sister-groups *Colidotea* and *Synisoma* are restricted to warm-temperate and subtropical waters of the New and Old World respectively (Fig. 12). This restriction, plus the widespread occurrence of *Synisoma* (Europe, Far East), suggests that these

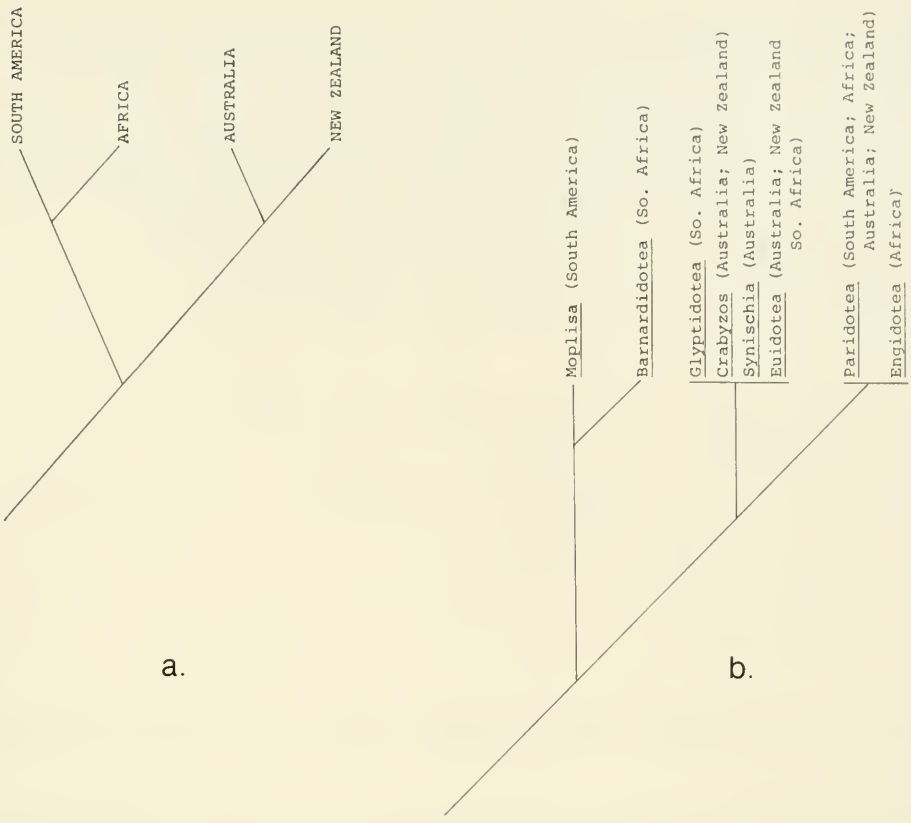


FIGURE 15**a**. Reduced geographic cladogram of 4 extant temperate shores derived from Gondwana (*see* Fig. 6). 15**b**. Reduced taxon-area cladogram of Southern Hemisphere endemic idoteine genera (*see* Fig. 3 and Table 2).

taxa are vicariant descendants of a widespread, circumglobal, northern Tethyian track. The absence of either of these genera on eastern American shores is most easily explained by local extinction on that coast. Closure of the Panama seaway in the Pliocene, or simple isolation from the parental stock as the North Atlantic opened up, could have provided the setting for the origin of these two taxa as we know them today. Judging by its extreme disjunct distribution, *Synisoma* has remained unchanged since at least the Paleocene, when the Gibralter gap closed. Thus, it appears that the ancestors of these two taxa were members of the Tethyian fauna, at least marginally, while the extant descendants have been pushed northward to the subtropical and warm-temperate portions of their former range.

In summary, the genera comprising lineage B appear to have remained closely tied to their ancestral (Jurassic) temperate Gondwanan distribution. Historical hypotheses that are consistent with the cladogram suggest that vicariance alone can account for the modern distributional patterns of only a few taxa, most having modern distributions clearly tied to both former vicariant and dispersal/extinction events. These probable extinctions, dispersal events, and biological interactions affecting ranges add to the uncertainty in ascribing geographic origins to the relatively old taxa comprising lineage B.

Turning to lineage A, we see one broadly distributed genus, the primitive *Zenobiana*, which occurs in both temperate and tropical waters of the Old World, but is restricted to temperate South America in the New World (Fig. 13). *Zenobiana* is the only genus of Idoteinae to retain the primitive biarticulate uropods. As was the case with *Idotea*, *Zenobiana*'s cladistic relationship and widespread distribution initially

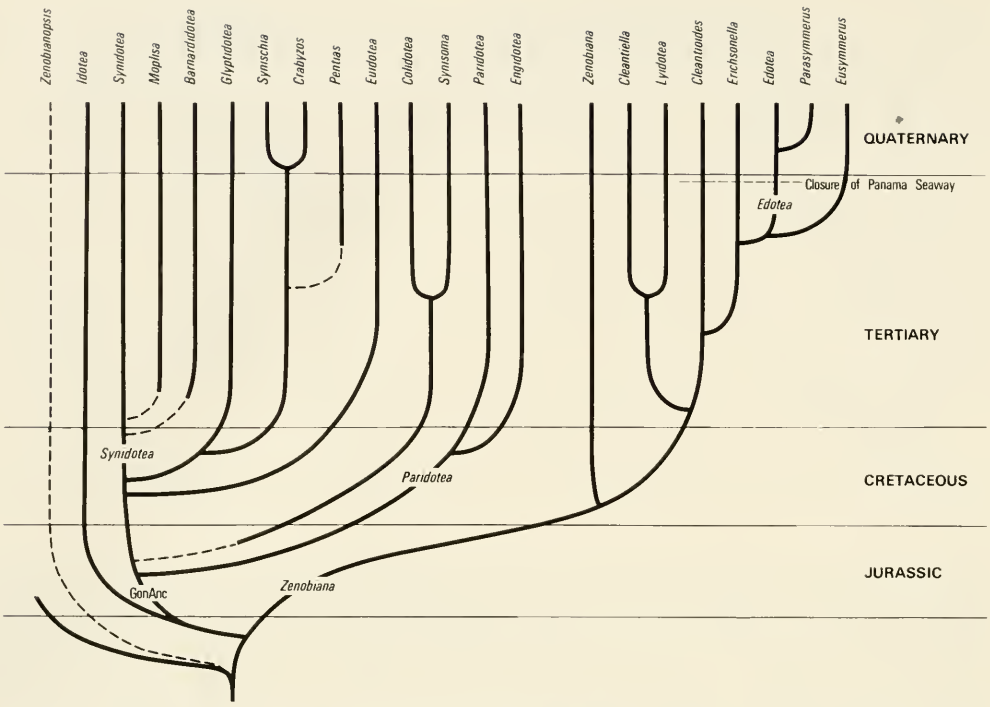


FIGURE 16. Proposed phylogeny of the genera of Idoteinae, based on Fig. 17 and other data. *See* text for discussion.

suggests that *Zenobiana* was pre- to Early Cretaceous in origin (i.e., pre-Gondwanan fragmentation). *Zenobiana* cannot be much older than this as it clearly shows no alliance to the Permo-Triassic Tethyian Sea radiation, owing to its near absence from the tropical Indo-West Pacific region; only one species occurs in Indo-Pacific waters, *Z. natalensis* (Barnard 1925). Thus, *Zenobiana*'s limited invasion of tropical environments apparently took place after the final closure of the Tethyian Sea, in the early to mid-Tertiary. Its alliance to and probable origin on temperate shores is further indicated by its present distributional pattern. All genera that appeared subsequent to the establishment of the globally distributed *Zenobiana* (the 7 remaining genera in lineage A) are warm-water taxa, or at least probably initially evolved as warm-water taxa (i.e., *Edotea*). The absence of identifiable apomorphies to distinguish *Zenobiana* indicates that this genus was both the ancestor to, and persisted after the origin of its sister-group.

Cleantioides consists of only 2 species: *C. occidentalis* is endemic to the tropical eastern Pacific; *C. planicauda* is a widespread tropical species known from both coasts of the Americas and from eastern Asia. *Cleantiella* and *Lyidotea* are western Pacific descendants of a *Cleantioides*-like ancestor. *Cleantiella* is restricted to the warm shores of USSR and China, and most likely arose as a post-Cretaceous northwest Pacific endemic (Fig. 8). *Lyidotea* is restricted to the warm waters of northeastern Australia. The absence of *Cleantiella* and *Lyidotea*, both warm-water taxa, from the equatorial region of the west Pacific is enigmatic and suggests 3 possibilities: (1) dispersal of the ancestor of *Lyidotea* from Asian shores to Australian shores; (2) the former existence of a N–S tropical *Cleantiella*-like track joining these two regions, with subsequent fragmentation into northern and southern tropical isolates with extirpation in the equatorial region; or (3) an artifact of collection records. The paucity of records for species in any other genus of Idoteidae from this region, and the unlikelihood of alternatives 1 and 2 above, suggest the third possibility may be the correct interpretation. According to Poore (in litt.) virtually no collecting has ensued in this region since the Siboga Expedition (ca. 1900).

All remaining genera in lineage A are New World endemics and represent descendants of the post-Cretaceous ancestors of this line. *Edotea* has an anti-tropical distribution, occurring on both North and South American shores (Fig. 14). Brusca and Wallerstein (1979*a*) have discussed this unusual distribution, concluding that *Edotea*, although evolving in the New World tropics as part of the early transisthmian track biota (the "Tertiary Caribbean Province" of Woodring 1954, 1966; the "Panamanian Track" of Croizat et al. 1974), was promptly excluded from this warm-water region by competition with the better adapted tropical genera like *Cleantioides*, *Eusymmerus*, *Parasymmerus*, and *Erichsonella*. Modern species of *Edotea* now occur only in temperate latitudes to the north and south of the New World tropics. "Better adapted" includes the possession of such predator avoidance adaptations as small body size, early reproduction, and cryptic morphologies (see Wallerstein and Brusca 1982, for details of these adaptations).

Edotea, *Erichsonella* (Fig. 14), and *Cleantioides* are all components of the Tertiary Caribbean Province (Woodring 1966) that have retained their amphi-American distributions. Numerous eastern Pacific-western Atlantic analog or geminate species can be identified within these genera. *Eusymmerus* and *Parasymmerus* (Fig. 14) are tropical eastern Pacific endemics. *Parasymmerus* probably evolved subsequent to the Pliocene closure of the Panama seaway. However, if the relationships depicted on the cladogram are correct, *Eusymmerus* probably evolved prior to the closure of the seaway (in order to be the sister-group or ancestor of *Edotea-Parasymmerus*). Its present restriction to the eastern Pacific implies that either (1) it evolved there and never became part of the transisthmian fauna, or (2) it was part of the transisthmian biota but has subsequently become extinct in the western Atlantic. The latter seems far the more probable sequence of events. Woodring (1966) has pointed out that many molluscan genera presently restricted to the tropical eastern Pacific occurred throughout the eastern Pacific-western Atlantic Tertiary Caribbean Province during Miocene times. These geographic data, as well as the cladistic relationships, imply that *Edotea* was both the ancestor to *Parasymmerus* and remained essentially unchanged subsequent to the origin of *Parasymmerus* (Fig. 16). It is unfortunate that fossil material for isopods is rare, for such data could provide excellent corroboration or refutation of the above hypothesis.[5]

The data summarized in the cladogram and biogeographic review clearly imply that there were both Old World and New World warm-water genera derived from an ancestral global "*Zenobiana-Cleantioides* line." The extant Old World fragments of this line are *Cleantiella* and *Lyidotea*; the extant New World fragments are *Erichsonella*, *Edotea*, *Parasymmerus*, and *Eusymmerus*.

The relationships in the cladogram suggest that these latter 4 New World endemic taxa were derived as the sister-group of *Lyidotea* (an Old World endemic). This necessitates trans-Pacific (west to east) dispersal of the ancestor of these 4 New World genera. An alternate scenario would have the New World taxa of lineage A descended not from the geographically restricted *Lyidotea* line or its Old World ancestor, but from the widespread ancestral *Zenobiana-Cleantioides* line. This could be accomplished simply by reconstructing a portion of lineage A, as shown in Fig. 17. This new cladogram of lineage A is longer than the original (Fig.4) in requiring 9 pleonal transformations, versus 8 in the original. The new cladogram requires four transformations (but two convergences) in maxillipedal palp reduction, as in the original. Thus, for lineage A we are faced with a cladogram slightly more parsimonious (one less step) but requiring a major successful trans-Pacific dispersal event to establish the entire New World tropical lineage of idoteine genera, versus a cladogram slightly less parsimonious but requiring only an easily explained vicariant origin of the New World line from a pre-drift cosmopolitan track. This is perhaps a case of strict methodological parsimony versus "biological parsimony." Given the multitude of avenues for pleonal reduction, I see no compelling reason to accept one cladogram over the other. Such problematic relationships can probably be resolved only by the elucidation of new generic-level attributes, and by careful examination of the morphological and biogeographic relationships of the individual species in these genera.

Discussion

The above phylogenetic and biogeographic analysis sheds light on several problems in understanding the evolution of the Idoteinae. First is the problem of discordant character trends. Although trends toward fusion of body somites and appendage articles (pleon, antennae, maxillipedal palp) have been noted for many decades, it was not until Menzies and Miller (1972) summarized and tabulated these data that the discordant trends in these different morphological features were recognized, suggesting probable high levels of homoplasy in the Idoteinae (see Table 1). Generating schematic pattern analyses (Figs. 4 and 17a) reveals that identical pleonal morphologies can be derived in a great many ways. For example, previous workers have assumed the 0+1 pleonal morphology of *Colidotea* to have been derived in the same manner as the 0+1 pleonal morphology of *Eusymmerus, Parasymmerus,* and *Edotea* (i.e., to be homologous), despite the fact that the former has a multiarticulate second antennal flagellum whereas the latter 3 genera have uniarticulate (clavate) second antennal flagella, the latter presumably being a fundamentally significant difference. In fact, the 0+1 pleonal morphology can be derived in any of about a dozen different ways, and in the above case it is clear that the derivation of *Colidotea* was probably quite different from that of the other 3 genera (see Figs. 3, 4, 16 and 17). Use of this schematic approach to pattern analysis in the Idoteinae also facilitates placement of the primitive genus *Zenobiana* in a single lineage apart from *Cleantioides,* even though both taxa have identical pleonal morphologies and have been confused with one another in the past. Further, the schematic analysis provides clear visual descriptions of all potential intermediate stage morphologies for the Idoteinae genera, lending high predictability (hence testability) to hypotheses contained in the above analysis.

That isopods, and peracarids in general, were already diverse and important taxa by the late Paleozoic has been fairly well documented by Schram (1970, 1974). By as early as the Pennsylvanian, the Peracarida had radiated into most if not all its currently recognized orders (except perhaps the Amphipoda). As Schram (1974) stated, ". . . peracarid radiation was probably initiated in Devonian time, when it is generally thought caridoid eumalacostracans were taking origin," ". . . the Peracarida are now known to be among the most ancient of the eumalacostracans," and ". . . the superorder Peracarida was a major element in the late Paleozoic radiation of eumalacostracans and contributed the principal caridoid types of that time." The earliest isopods known from the fossil record are phreatoicids from the middle Pennsylvanian; spelaeogriphacians, tanaids, and mysidaceans first appear in the lower Carboniferous.

The origins of the subfamilies of Idoteidae hypothesized in this study are consistent with Schram's data, and also with dates offered by Schultz (1979), who stated that most isopod families were well-defined before the Triassic.

The present analysis reveals the existence of two principal lines of descent within the Idoteinae (Fig. 16), lines that separated from one another early on (Jurassic or perhaps even Triassic). One of these lines remained closely tied to its origins in the Old World Southern Hemisphere temperate biota, while the other invaded New World environments and undertook a radiation in the New World tropics (producing genera such as *Cleantioides, Erichsonella, Eusymmerus,* and *Parasymmerus*). Brusca and Wallerstein (1979*b*) hypothesized that idoteids might only recently have invaded the New World tropics, perhaps in close association with a similar invasion of these regions by the brown algae (Phaeophyta), which probably serve as the principal habitat and food resource for most idoteine species. That the late Triassic-Early Jurassic periods might have had a widespread southern temperate Idoteinae distribution of little or no endemism is hardly surprising. As Hallam (1981) points out, Jurassic marine faunas as a whole were decidedly more cosmopolitan than those of the present day. These early origins in temperate waters explain the long-held belief that the Idoteidae and Idoteinae are "cold-water centered taxa." Plate movements became increasingly influential in promoting endemism within the Idoteinae from Late Jurassic through Late Cretaceous, as Pangaea fragmented. The high degree of endemism among Idoteinae genera contrasts

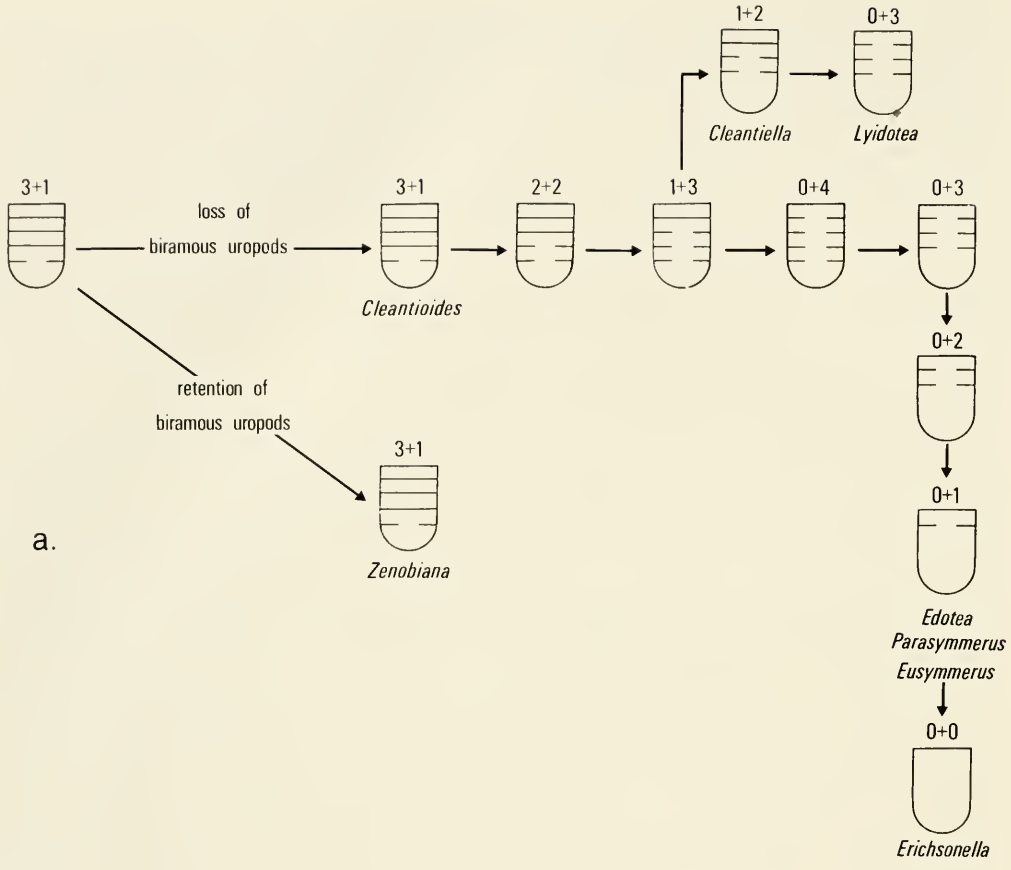
sharply with claims by Taylor and Forester (1979) that cold-water psychrospheric isopod biofacies (generic assemblages) tend to be similar regardless of latitude or depth.

This study has shed some light on the place of origin of both the Idoteinae and the Idoteidae, as well as the Valvifera itself. Distributions of the Idoteidae subfamilies (excluding the Idoteinae) are given in Fig. 18; distributions of the five other valviferan families are given in Fig. 5. As can be seen, two of the five Idoteidae subfamilies are distinctly Gondwanan in distribution (Glyptonotinae and Chaetilinae), one is predomintly Laurasian (Mesidoteinae), one is ubiquitous (Idoteinae), and one is endemic to the shores of Morocco (Parachiridoteinae). Of the six valviferan families, two are cosmopolitan (Idoteidae and Arcturidae), and the remaining four are all Gondwanan, including the most primitive family, the Holognathidae. No valviferan family is distinctly Laurasian in distribution. These data taken together strongly suggest that the Valvifera originated in the temperate Southern Hemisphere at least by early or mid-Pangaean times (Permian/Triassic), if not earlier.

Hurley and Jansen (1977) reviewed the zoogeography of the isopod family Sphaeromatidae on Southern Hemisphere coastlines. Their data on generic and species distributions reflect patterns similar to those seen here in the Idoteinae. Hurley and Jansen found generic affinity between all southern continents, as well as generic endemism on all shores (endemism levels reported are 12 genera [48%] in Australia; 7 genera [41%] in South Africa; 3 genera [20%] in New Zealand; and 1 genus [11%] in Chile). Hurley and Jansen invoked strict dispersalist mechanisms to account for these distributions, however, and stated, "The possibility of invoking continental drift as an agency is hardly necessary in view of the fact that littoral species are involved." What this statement is meant to imply is not clear. Presumably the authors are suggesting that littoral organisms are expected to disperse across ocean barriers with great regularity, thus negating the roles of continental drift and vicariance in establishing endemism. This view seems inconsistent with their data, however, which record high levels of endemism at both generic and species levels on southern continental shores (species endemism on Australian shores was reported as 91%; South African shores, 80%; New Zealand, 89%; Chile, 62%). In any event, Hurley and Jansen (1977) did not present any phylogenetic analyses of the taxa in question, making it impossible to evaluate alternative biogeographic scenarios for the Southern Hemisphere Sphaeromatidae.

The present study reveals several situations wherein ancestral taxa apparently persisted while new (sister) taxa evolved as peripheral isolates (or perhaps in sympatry) in restricted geographic regions. For example, *Synidotea* almost certainly persisted unchanged during the events that produced *Moplisa* and *Barnardidotea*. Similar situations exist for: *Paridotea* and *Engidotea*; *Zenobiana* and its sister-group; and *Edotea* and *Parasymmerus* (see Fig. 16).

This study suggests that both dispersal and vicariant forces probably played important roles in creating modern-day distributional patterns of idoteine genera. Dispersal via the Antarctic Circumpolar Current appears to have played only a minor role, however, as endemism on southern shores is high. The unique (highly endemic) nature of these southern continental shores was established long ago. Even New Zealand, which spans 13 degrees of latitude and sits just 1760 km off Australia, is noted for its high endemicity of coastal species. Examples include 24% endemism for polychaetes (Augener 1924), 50% for crabs (Chilton and Bennet 1929), 64% for echinoderms (Mortensen 1925), and 89% for sphaeromatid isopods (Hurley and Jansen 1977). Because the present analysis was at the generic level rather than the species level, and because several Southern Hemisphere genera cannot be clearly distinguished in a cladogram, resolution of all geographic patterns has not been achieved. What is clearly needed are similar analyses for each of the idoteine genera (e.g., see Brusca 1983). It is of particular interest to note that the major lines of descent within the Idoteinae appeared prior to the mid- to Late Cretaceous global warming trend, no doubt further facilitating the temperate-based distribution of this taxon. The present study adds further evidence to a large body of data demonstrating the concept of the Crustacea being a taxon fraught with convergences. As Schram (1978) deftly pointed out, "The central dominating



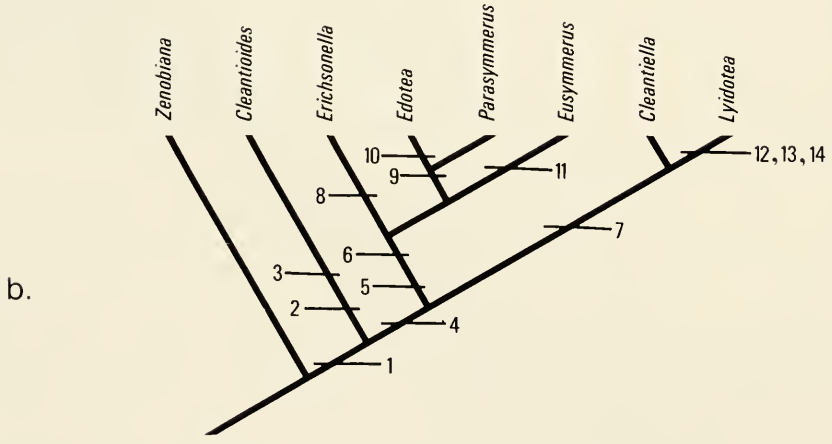


FIGURE 17**a**. Alternative schematic representation for lineage A, based on biogeographic analysis. 17**b**. Alternative cladogram for lineage A, based on 17**a**. Synapomorphies are as follow: (1) uropods uniramous, (2) pereopods IV reduced, (3) maxillipedal palp reduced in some species to 4 articles, (4) pleon 2+2, (5) maxillipedal palp reduced to 4 articles, (6) pleon 0+1, (7) pleon 1+2, (8) pleon 0+0, (9) maxillipedal palp reduced to 3 articles, (10) pleon with unique, acute, subtriangular shape, (11) left mandible with 3-pointed spine arising between lacinia and incisor, (12) pereonite VII fused to pleonite 1, (13) maxillipedal palp reduced to 3–4 articles, (14) pleon 0+3. *See* text for discussion.

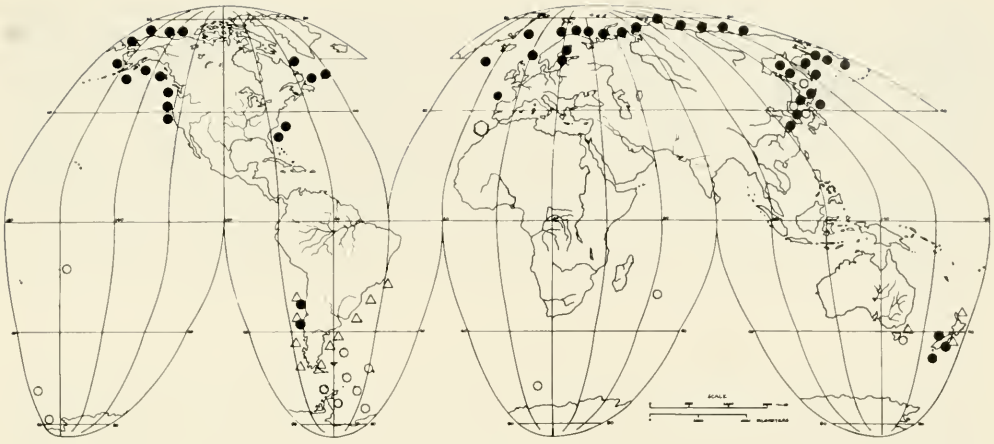


FIGURE 18. Distribution of the subfamilies of Idoteidae (except Idoteinae): Mesidoteinae [●], Chaetilinae [△], Glyptonotinae [○], Parachiridoteinae [○].

theme of arthropod evolution is the multiplicity of convergent development. No phyletic scheme, monophyletic or polyphyletic, can escape this."

Wiley (1981) divided biogeography into three subdisciplines: descriptive, historical, and ecological biogeography. He felt that the goals and interests of the ecological biogeographer lie more with ecology than with systematics, whereas the opposite is true of the historical biogeographer. Finally, he suggested that systematics has little to contribute directly to the field of ecological biogeography. I disagree with Wiley, and feel I have shown here and through a series of studies that there is a logical sequence of basic taxonomy/descriptive biogeography/ecological-historical biogeography, all these studies existing within the realm of systematics (i.e., Brusca and Wallerstein 1977, 1979*a*, *b*, Wallerstein and Brusca 1982, Brusca 1983). Hessler and Wilson (in press) provide further evidence of these relationships by their implication of both ecological and historical factors in reviewing the probable causes for differences in distribution of major crustacean taxa. Pregill and Olson (1981) came to similar conclusions with regards to the Caribbean land vertebrates, as did Stock (1981) regarding the Caribbean crustacean stygobionts. While the methods of ecological and historical biogeography may differ, the two endeavors are clearly complementary; to attempt one at the expense of the other is to invite error.

Only a few genera of Idoteinae can be confidently tied to vicariance events associated with the breakup of Pangaea. Only one New World genus (*Parasymmerus*) can be clearly tied to such major geological events. Vicariant relationships seem to be more easily distinguished at the species level (*see* Brusca 1983). It would seem that, at least in idoteid isopods, too much time has passed and too many unknowable events transpired (new taxa have evolved and gone extinct, extant taxa have undergone local extinctions in selected portions of their range, dispersal events, etc.) to confidently extract clear vicariant patterns at the level of supraspecific taxa. Furthermore, those idoteine taxa that do appear to be products of vicariance phenomena can only be tested by comparison to cladograms and distributional data for other intertidal groups. Cracraft (1982) has recently detailed such a procedure. Briefly, allopatric vicariant speciation (type 1a of Bush 1975) implies the appearance of a barrier. In the case of littoral isopods, these barriers would be new stretches of ocean or new land barriers across shallow seaways. Such a barrier would be expected to influence the vicariance patterns of numerous intertidal taxa, and one would thus predict that concordant pairs of sister-taxa would exist on either side of the barrier. In contrast, speciation resulting from a dispersal event to a new area (a founder individual or population; type 1b speciation of Bush 1975) is generally taken to be a random event. Hence, one would predict not

to find concordant vicariance patterns from one clade to another. Absence of such concordance with other intertidal taxa thus would suggest that speciation was initiated not by a vicariance event, but by a dispersal event. Thus, the need for cladograms of other marine invertebrate groups becomes evident, and without such studies one cannot critically assess the hypothesized processes responsible for the patterns present today in the idoteine taxa. Finally, the low levels of congruence between the cladogram of taxa-area and geographic cladogram can also be explained by the simple hypothesis that Gondwanan distributions of ancestral idoteid taxa were NOT widespread, but fragmented and local. This possibility, of course, denies a popular premise of generalized tract theory, that ancestral ranges can be assumed to be the sum of the ranges of the descendants.

Footnotes

[1] There have been several recent attempts to cast doubt on the monophyletic nature of the Peracarida (Watling 1981, Dahl and Hessler 1982, Hessler in press). This is not the place to present detailed analyses and criticisms of each of these studies. However, it should be pointed out that in Watling's "cladistic" analysis only certain selected characters were used, numerous character transformations were illogical and unexplained, character states attributed to various taxa were incorrect, and a clear method of character polarity assessment was not provided. Although the other recent studies (op. cit.) employed a variety of approaches, often in the guise of cladograms, none attempted to analyze character state polarities in a strict logical order or with any clearly expressed methodology. Schram (1981) was concerned with the recognition of basic structural plans within the Eumalacostraca, and his classification is based on a strictly random array of character associations. The phenogram he chose for conversion into a classification is the one he felt "most comfortable with." Hessler's (in press) "cladogram" of the Peracarida (his fig. 5) is entirely unjustified by the data he presents. Among other problems, no attempt was made to achieve parsimony and the "cladogram" actually requires more convergences (at least 24) than its contained character transformations (23). In the case of Watling (1981) and Hessler (in press) it appears as though evolutionary scenarios were conceived first, these then being transformed into dendrograms (incorrectly called cladograms) upon which the appropriate "apomorphies" were overlain. Hessler's dendrogram of the Peracarida is essentially Siewing's (1963 and earlier publications) concept of peracarid relationships. This procedure, of course, ignores parsimony considerations and is the exact reverse of what a phylogenetic (cladistic) analysis is meant to accomplish.

The fact is, there exist many unique synapomorphies that unite the peracarid orders: (1) maxilliped with basis produced into an anteriorly directed, bladelike endite; (2) lacinia mobilis present in adults; (3) oostegites formed on inner pereopodal coxal margin; (4) young brooded in a brood chamber or "marsupium" (the location of the brood chamber varies from a simple oostegial pouch to invaginations of the sterna, modified oviducts, or even to the inner carapace region in the thermosbaenaceans); (5) direct development, with no true postnaupliar larval stages; (6) release of the young as "manca"; (7) whiplike immobile sperm, devoid of fibrils and mitochondria (this character needs further documentation); (8) a large suite of embryological attributes (*see* below); and (9) a large suite of attributes associated with the functional morphology of the pereopods. These functional and morphological skeletomuscular adaptations are associated with a system unique to the Peracarida, in which the body-coxa articulation has lost the caridoid "gimbal" joint and become either immobilized or capable of only limited abduction/adduction, and the coxa-basis articulation become monocondylic but capable of performing a complete suite of motions. This peracaridan system for ambulation is present in the incipient condition in mysidaceans. Hessler (1982) views these particular peracaridan leg synapomorphies as adaptations necessitated by the development of the marsupium and its attendant oostegites. Although thermosbaenaceans have lost the oostegites, they still retain the infolded monocondylic articulation of the pereopodal coxa and basis (*see* Hessler 1982, for details).

The loss of the oostegites in the thermosbaenaceans is probably a response necessitated by unique morphological (fusion of pereopodal articles) and functional (locomotory) adaptations of the pereopodal endites in this group. Loss of oostegites and concomitant relocation of the brood chamber is not unique to the thermosbaenaceans among the Peracarida (it occurs in several hyperiid amphipods and isopod higher taxa). This matter has been competently dealt with by Fryer (1964) and need not be repeated here (also *see* Hessler 1982 and Siewing 1958).

The presence of lacinia-like movable spines in the larvae of a few species of euphausids and shrimps suggests two possibilities: (1) the lacinia of adult peracarids is a paedomorphic attribute (*sensu* Gould 1977) retained from a nonperacaridean ancestor with lacinia in larval stages only, or (2) these are superficially similar convergent features. The absence of postnaupliar larval stages in the Peracarida, and their direct development to a juvenile hatching stage, argue for their origin not from a eucarid ancestor but from a line separate from the eucarids. Hence, the second hypothesis is the more parsimonious. The structural simplicity of the "lacinia" of eucarid larvae, versus the complexity of the peracarid lacinia supports this contention. Should one choose to consider the movable mandibular spine of certain adult bathynellaceans to be true lacinia (*see* Siewing 1963, Schminke 1972, and Dahl and Hessler 1982), one is confronted again with two possibilities: (1) the adult lacinia is a feature representing a potential synapomorphy for a bathynellacean-peracarid line, or (2) this character is convergent in these two groups. I would accept either interpretation as a working hypothesis. The latter seems the more likely considering the presence of movable spines in certain eucarid larvae and the apparent plasticity of the spines of the mandibular row. The point is, however, that acceptance of either hypothesis would not affect the monophyletic status of the Peracarida! Frankly,

with regards to the monophyly of the Peracarida, all the fuss over the lacinia seems "much ado about nothing."

The Peracarida retain an "underlying unity in development" (Anderson 1973) distinct in numerous ways from the Eucarida and Syncarida. This unity has been well documented and succinctly summarized by Anderson (1973). Unique attributes of peracaridan development appear in virtually all stages of embryogenesis, and include among other things: the early segregation of primordial germ cells as a definite presumptive area; the teloblastic development of the postnaupliar segments; the vitellophage modifications in the early development of the midgut, the unique embryogeny of the digestive glands; the distinct embryogeny of the ectoderm; and the formation of a second pair of "dorsal organs" (the ectodermal dorsolateral organs).

The "mancoid" stage appears to be little more than the product of alterations in embryogeny and timing in the release of the young. Its absence in mysids and amphipods may be tied to a more rapid embryological development (or to a delayed postembryonic development) in these two taxa (*see* Steele and Steele 1975), which may also be linked to the presence of ventrally curved embryos and completion of cleavage in the early stages in these groups (i.e., rapid early holoblastic cleavage). Furthermore, although amphipods leave the marsupium with all 7 pairs of pereopods "in place," there is a great deal of variation in the structure and development of this appendage, particularly in the hyperiids. Laval (1980) has even recognized hyperiid "larvae," with distinct hatching stage morphologies. Much of the distinction between Laval's "larvae" and the adults involves the nature of the pereopods, and some hyperiids certainly appear to have "virtual mancoids." The seventh pereopods seem especially plastic in hyperiids and amphipods in general. The rudimentary nature of the seventh pereopods in "juvenile" amphipods of certain species has been known at least since the work of Bate (1861) on *Vibilia*. One could also posit the origin of the mancoid stage subsequent to the origin of the mysids and amphipods during peracaridan cladogenesis. This would remove this attribute from the list of synapomorphies defining the Peracarida, but it would certainly not destroy the monophyletic nature of that taxon; rather, it would simply make the "mancoid stage" a synapomorphy defining a subset within the Peracarida.

An embryological attribute that might suggest alliance among the amphipods, mysids and eucarids is the retention (from the larval stages) of the functional antennal glands in these three taxa. Since all Crustacea have antennal glands during their embryogeny, the retention of these glands into adulthood in these taxa hardly seems surprising and is most likely either a convergence or simply a symplesiomorphy retained from a common ancestor (i.e., a plesimorphy not lost until the appearance of the mysids and amphipods had been achieved during peracaridan cladogenesis).

I believe that a carefully (and correctly) accomplished cladistic analysis of the Peracarida will reveal the amphipods to be the nearest relative if not the sister-group of the isopods. No such analysis has been published to date, although one is in preparation by F. Schram. Watling (1981), Hessler (in press) and others have chosen to ignore or deemphasize the fundamental synapomorphies unique to these two taxa (e.g., sessile compound eyes; pereonites with coxal plates; pereopods entirely uniramous; carapace entirely lost; mandible of the transverse biting type), and rely instead on differences and retained plesiomorphies in their analyses. As indicated in Fig. 2, I do not believe that there are ANY shared derived characters unique to the tanaids-isopods.

[2] Note that were the amphipods taken to be the sister-group to the isopods, attributes 1, 2 and 4 would become synapomorphies uniting these two taxa.

[3] The genus *Austridotea* is in need of further study; it may have to be removed to the Idoteinae.

[4] Poore (in litt.) has suggested that the 4 non-idoteine subfamilies are synonymous and should be combined. At the time of this writing I am in general agreement with Poore, but do not address the matter here.

[5] The single Old World species of *Edotea* (*E. dilatata* Thomson, 1884) has been shown to be the female of *Crabyzos elongatus* (Miers 1876) (*see* Hurley 1961:292).

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Literature Cited

Addicott, W. O. 1970. Tertiary paleoclimatic trends in the San Joaquin Basin, California. U. S. Geol. Survey, Professional Pap. 644-D. 19 pp.

Anderson, D. T. 1973. Embryology and Phylogeny in the Annelids and Arthropods. Pergamon Press, New York. 495 pp.

Augener, H. 1924. Polychaete von den Auckland- und Campbell-Inseln. Vid. Meddel. Dansk Naturhist. Foren. 75:1–116.

Barnard, K. H. 1920. Contributions to the crustacean fauna of South Africa. No. 6. Further additions to the list of marine Isopoda. Ann. So. African Mus. 17(11):319–438.

Barnard, K. H. 1925. Contributions to the crustacean fauna of South Africa. No. 9. Further additions to the list of Isopoda. Ann. So. African Mus. 20(5):381–410.

Bate, C. S. 1861. On the morphology of some Amphipoda of the division Hyperina. Ann. Mag. Naturl. Hist. (Ser. 3) 8:1–16.

———, and J. O. Westwood. 1861–1868. A History of the British-Sessile-Eyed Crustacea. London. John Van Voorst. [in 23 parts; 1 Oct 1861–31 Dec 1868] 536 pp.

Benedict, J. E. 1897. A revision of the genus *Synidotea*. Proc. Acad. Natural Sci. Philadelphia 49:389–404.

Brandt, J. F. 1833. Conspectus monographie Crustaceorum Oniscordorum Latreilli. Bull. Soc. Imp. Nat. Moscou 6:171–193.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill, New York. 475 pp.

Brown, A. C., and N. Jarman. 1978. Coastal marine habitats. *in* J. Werger (ed.). Biogeography and Ecology of Southern Africa, Vol. II. Junk, Lochem, Holland. 1434 pp.

Brown, Jr., W. L. 1965. Numerical taxonomy, convergence and evolutionary reduction. Syst. Zool. 14:101–109.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by the chironomid midges, with a monograph of the subfamily Podonominae, Aphrotaenidae and the austral Heptagiae. Kungliga Svenska Vetenskapsakademiens Handlingar 4(11):1–472.

———. 1970. Antarctic land faunas and their history. Pp. 42–53 *in* M. M. Holdgate, (ed.). Antarctic Ecology, Vol. 1. Academic Press, New York.

———. 1972*a*. Circum-Antarctic distribution patterns and continental drift. 17th Internat. Zool. Cong., Theme 1:1–11.

———. 1972*b*. Phylogenetics and biogeography. Syst. Zool. 21:69–79.

———. 1976. A neocomian chrionomid and Podonominae-Aphroteiinae (Diptera) in the light of phylogenetics and biogeography. Zoologica Scripta 5(3–4):139–160.

Brusca, R. C. 1983. Two new idoteid isopods from Baja California and the Gulf of California (Mexico) and an analysis of the evolutionary history of the genus *Colidotea* (Crustacea: Isopoda: Idoteidae). Trans. San Diego Naturl. Hist. Mus. 20(4):69–79.

———, and B. R. Wallerstein. 1977. The marine isopod crustaceans of the Gulf of California. I. Family Idoteidae. Amer. Mus. Novitates, No. 2634:1–17.

———, and B. R. Wallerstein. 1979*a*. The marine isopod crustaceans of the Gulf of California. II. Idoteidae. New genus, new species, new records and comments on the morphology, taxonomy and evolution within the family. Proc. Biol. Soc. Wash. 92(2):253–271.

———, and B. R. Wallerstein. 1979*b*. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow-water zoogeography for the region. Bull. Biol. Soc. Wash. 3:67–105.

Bush, G. L. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst. 6:339–364.

Calman, W. T. 1909. A Treatise on Zoology. Part VII. Appendiculata, Crustacea. R. Lankester (ed.). London. Adam and Charles Black. 346 pp. [reprinted by A. Asher and Co., Amsterdam, 1964].

Chilton, D. 1890. Revision of the New Zealand Idoteidae. Trans. New Zealand Inst. 22:189–204.

Cracraft, J. 1974. Phylogeny and evolution of the ratite birds. The Ibis 116(4):494–541.

———. 1980. Biogeographic patterns of terrestrial vertebrates in the southwest Pacific. Paleogeogr., Palaeoclim., Paleoecol. 31:353–369.

———. 1982. Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. Amer. Zool. 22(2):411–424.

Chilton, C., and E. W. Bennett. 1929. Contribution for a revision of the Crustacea Brachyura of New Zealand. Trans., Proc. New Zealand Inst. (Wellington) 59:731–778.

Collinge, W. E. 1917. A revision of the British Idoteidae, a family of marine isopods. Trans. Roy. Soc. Edinburgh 60:721–760.

Crawford, A. R. 1974. A greater Gondwanaland. Science 184:1179–1181.

Croizat, L., G. Nelson, and D. E. Rosen. 1974. Centers of origin and related concepts. Syst. Zool. 23(2):265–287.

Dahl, E., and R. R. Hessler. 1982. The crustacean lacinia mobilis: a reconsideration of its origin, function and phylogenetic implications. Zoo. J. Linn. Soc. 84:133–146.

Dana, J. 1853. On the geographical distribution of Crustacea. Pp. 696–805 *in* United States' Exploring Expedition during the years 1838–1842, under the command of Charles Wilkes, U.S.N., Vol. 14, No. 2. Crustacea. Pp. 696–805.

de Jong, R. 1980. Some tools for evolutionary and phylogenetic studies. A. Zool. Syst. Evolut.-Forsch. 18:1–23.

Durham, J. W. 1979. The fossil record, plate tectonics, and development of characteristic

members of austral marine faunas. Pp. 165–186 *in* N. Z. DSIR [cited below].

Ekman, S. 1953. Zoogeography of the Sea. London. Sidgwick and Jackson. 417 pp.

Eldredge, N., and J. Cracraft. 1979. Introduction to the symposium. Pp. 1–5 *in* J. Cracraft, and N. Eldredge (eds.). Phylogenetic Analysis and Paleontology. Columbia Univ. Press, New York. 233 pp.

———, and ———. 1980. Phylogenetic Patterns and the Evolutionary Process. Method and Theory in Comparative Biology. Columbia Univ. Press, New York. 349 pp.

Endler, J. A. 1982. Problems in distinguishing historical from ecological factors in biogeography. Amer. Zool. 22:441–452.

Felsenstein, J. 1973. Maximum-likelihood estimation of evolutionary trees from continuous characters. Amer. J. Hum. Genet. 25:471–492.

Fleming, C. A. 1962. New Zealand biogeography: a paleontologist's approach. Tuatora 10(2):53–108.

———. 1975. The geological history of New Zealand and its biota. Pp. 1–86 *in* G. Kuschel (ed.). Biogeography and Ecology in New Zealand. Monogr. Biol. 27. W. Junk, The Hague.

———. 1979. The Geological History of New Zealand and Its Life. Auckland Univ. Press. 141 pp.

Frakes, L. A. 1979. Climates Throughout Geologic Time. Elsevier Scientific Publishing Co., N.Y. 310 pp.

Fryer, G. 1964. Studies on the functional morphology and feeding mechanisms of *Monodella argentarii* Stella (Crustacea: Thermosbaenacea). Trans. Roy. Soc. Edinburgh 66:49–90.

Gould, S. J. 1977. Ontogeny and Phylogeny. The Belknap Press, Harvard Univ. Press, Cambridge. 501 pp.

Grant-Mackie, J. A. 1979. Cretaceous-Recent plate tectonic history and paleoceanography development of the Southern Hemisphere. Pp. 27–42 *in* N. Z. DSIR [cited below].

Gurjanova, E. F. 1935. Zur zoogeographie de Crustacea Malaconstraca des Arktischen gebietes. Zoogeographica 2:555–571.

Hallam, A. 1981. Relative importance of plate movement, eustasy and climate in controlling major biogeographical changes since the early Mesozoic. Pp. 303–330 *in* G. Nelson, and D. E. Rosen (eds.). Vicariance Biogeography—A Critique. Columbia Univ. Press, New York. 593 pp.

Harger, O. 1880–1881. Report on the marine Isopoda of New England and adjacent waters. Rpt. U.S. Comm. Fish & Fisheries, 1878, Pt. 6:297–462. Washington, D.C.

Harper, C. W., Jr. 1979. A Batesian probability view of phylogenetic systematics. Syst. Zool. 28:547–553.

Hatch, M. H. 1947. The Chelifera and Isopoda of Washington and adjacent regions. Univ. Wash. Publ. Biology 10(5):155–247.

Hennig, W. 1966. Phylogenetic Systematics. Translated by D. Dwight Davis and Ranier Zangerl. Univ. Illinois Press, Urbana. 263 pp.

Hessler, R. R. 1982. The structural morphology of walking mechanisms in eumalacostracan crustaceans. Phil. Trans. Royal Soc. London (Ser. B) 296: 245–298.

———. in press. A defense of the caridoid facies; wherein the early evolution of the Eumalacostraca is discussed. Pp. 145–164 *in* F. R. Schram, (ed.). Crustacean Phylogeny. Balkema Publs., Rotterdam.

———, and G. D. Wilson. in press. The origin and biogeography of malacostracan crustaceans in the deep sea. Spec. Publ. Syst. Assoc. (London). [Proc. Internat. Symp. on Biogeogr. "Time and Space in the Emergence of the Biosphere" London, 1981]

———, ———, and D. Thistle. 1979. The deep-sea isopods: a biogeographic and phylogenetic overview. Sarsia 64:67–75.

Hooker, J. D. 1853. The botany of the Antarctic voyage of H. M. Ships *Erebus* and *Terror* in the years 1838–1843. Pt. II. Flora Novae-Zealandiae, Vol. 1. Lovell Reeve, London. 312 pp.

———. 1860. On the origin and distribution of species: introductory essay to the flora of Tasmania. Amer. J. Sci. & Arts (2)29:1–25, 305–326.

Hull, D. L. 1979. The limits of cladism. Syst. Zool. 28(4):416–440.

Hurley, D. E., and K. P. Jansen. 1977. The marine fauna of New Zealand: Family Sphaeromatidae (Crustacea: Isopoda: Flabellifera). Mem. New Zealand Oceanogr. Inst. 63:1–95.

Huxley, T. H. 1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. Proc. Zool. Soc. London, 1868: 294–319.

Issell, R. 1913. Richerche de etologie sull'Isopodo tubicola *Zenobiana prismatica* (Risso). Arch. Zool. Exper. Gen. 51:450–479.

Jansson, A.-M., and A.-S. Matthiesen. 1971. On the ecology of young *Idotea* in the Baltic. Pp. 71–88 *in* D. J. Crist (ed.). Fourth European Mar. Biol. Symposium, Cambridge Univ. Press. 599 pp.

Keast, A. 1973. Contemporary biota and the separation sequence of the southern continents. Pp. 309–343 *in* D. H. Tarling, and S. K. Runcorn (eds.). Implications of Continental Drift to the Earth Sciences. Vol. 1. Academic Press, New York. 622 pp.

Kennett, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. J. Geophysical Res. 82(27):3843–3860.

Kitts, D. B. 1981. (Review of . . .) N. Eldredge and J. Cracraft. Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology. 1980. Columbia Univ. Press. Science 210:1239–1240.

Knox, G. A. 1975. The marine benthic ecology and biogeography. Pp. 353–403 *in* G. Kuschel (ed.). Biogeography and Ecology in New Zealand. Monogr. Biol. 27. W. Junk, The Hague.

———. 1979. Distribution patterns of Southern Hemisphere marine biotas: some comments on their origins and evolution. Pp. 43–82 *in* N.Z. DSIR [cited below].

Laval, P. 1980. Hyperiid amphipods as crusta-

cean parasitoids associated with gelatinous zooplankton. Oceanogr. Mar. Biol. Ann. Rev. 18:11–56.

Lee, W. L., and B. M. Gilchrist. 1972. Pigmentation, color change and the ecology of the marine isopod *Idotea resecata* (Stimpson). J. Exp. Mar. Biol. Ecol. 10:1–27.

Margolis, S. V., P. M. Kroopnick, and D. E. Goodney. 1978. Cenozoic and late Mesozoic paleoceanographic and paleoglacial history recorded in circum-Antarctic deep-sea sediments. Mar. Geol. 25:131–147.

McDowall, R. M. 1978. Generalized tracks and dispersal in biogeography. Systematic Zool. 27(1):88–103.

Menzies, R. J. 1950*a*. The taxonomy, ecology and distribution of northern California isopods of the genus *Idothea* with the description of a new species. Wasmann J. Biol. 8(2):155–195.

———. 1950*b*. A remarkable new species of marine isopod, *Erichsonella crenulata* n. sp., from Newport Bay, California. Bull. So. Calif. Acad. Sci. 49:29–35.

———, and T. E. Bowman. 1956. Emended description and assignment to the new genus *Ronalea* of the idotheid isopod *Erichsonella pseudoculata* Boone. Proc. U.S. Nat. Mus. 106(3371):339–445.

———, and D. Frankenberg. 1966. Handbook on the Common Marine Isopoda of Georgia. Univ. Georgia Press, Athens. 93 pp.

———, and M. A. Miller. 1972. Systematics and zoogeography of the genus *Synidotea* (Crustacea: Isopoda) with an account of California species. Smithsonian Contrb. Zool. No. 102: 1–33.

———, and R. J. Waidzunas. 1948. Postembryonic growth changes in the idopod *Pentidotea resecata* (Stimpson), with remarks on their taxonomic significance. Bio. Bull. 95:107–113.

Miers, E. J. 1881. Revision of the Idoteidae, a family of sessile-eyed Crustacea. J. Linn. Soc. London 16:1–88.

Milne Edwards, H. 1840. Histoire Naturelle des Crustacés, comprenant 'anatomie, la physiologie et la classification de ces animaux. Librairie Encyclopédique de Roret, Paris 3:120–283.

Morse, J. C. and D. F. White, Jr. 1979. A technique for analysis of historical biogeography and other characters in comparative biology. Syst. Zool. 28(3):356–365.

Mortensen, T. 1925. Echinoderms of New Zealand and the Auckland-Campbell Islands, III–V. Vid. Medd. Dansk Naturh. Foren 79:261–420.

Naylor, E. 1972. British Marine Isopods. Academic Press, London. 86 pp. [Synopses of the British Fauna, n. ser., No. 3, The Linnean Soc. London.]

Nelson, G. and N. Platnick. 1981. Systematics and Biogeography. Columbia Univ. Press, New York. 567 pp.

Nordenstam, A. 1933. Marine Isopoda of the families Serolidae, Idotheidae, Pseudidotheidae, Arcturidae, Parasellidae, and Stentriidae mainly from the South Atlantic. Further Results of the Swedish Antarctic Exped., 1901–1903 3(1):1–284.

Norton, I. O., and J. G. Sclater. 1979. A model for the evolution of the Indian Ocean and the breakup of Gondwanaland. J. Geophysical Res. 84(B12):6803–6830.

N.Z. DSIR. 1979. Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere. Auckland, New Zealand. 17–20 July 1978. Vol. 1 & 2. New Zealand Dept. Sci. Indust. Res. (N.Z. DSIR), Information Ser. No. 137.

Ohlin, A. 1901. Isopoda from Tierra del Fuego and Patagonia. I. Valvifera. Svenska Esped. till Magellandslanderna 2(11):261–306.

Pantin, C. F. A., et al. 1960. A discussion on the biology of the southern cold-temperate zone. Proc. Royal Soc. London 152B:429–682.

Platnick, N. I. 1979. Philosophy and the transformation of cladistics. Syst. Zool. 28:537–546.

Poore, G. C. B. 1981. Marine Isopoda of the Snares Islands, New Zealand—1. Gnathiidea, Valvifera, Anthuridea, and Flabellifera. New Zealand J. Zool. 8:331–348.

Pregill, G. K., and S. L. Olson. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. Ann. Rev. Ecol. Syst. 12:75–98.

Racovitza, E. F., and R. Sevastos. 1910. *Proidotea haugin* g., n. sp. Isopode Oligocene de Roumanie et les Mesidoteini Nouvelle Sousfamille des Idotheidae. Arch. Zool. Exper. Gen. 46(5): 175–200.

Raven, P. H., and D. I. Axelrod. 1972. Plate tectonics and Australasian paleogiogeography. Science 176:1379.

Richardson, H. R. 1899*a*. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two new species. Proc. U.S. Nat. Mus. 21:815–869.

———. 1899*b*. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two new species. Ann. Mag. Nat. Hist. 4(7):157–187, 260–277, 321–338.

———. 1900. Synopsis of North American invertebrates. VIII. The Isopoda. Amer. Naturalist 34:207–230.

———. 1901. Key to the isopods of the Atlantic coast of North America with descriptions of new and little known species. Proc. U.S. Nat. Mus. 23:493–579.

———. 1904. Isopod crustaceans of the northwest coast of North America. Harriman Alaska Exped., Crustacea 10:213–230. [Reprinted: Richardson, H., 1904, Contributions to the natural history of the Isopoda, 2nd part, Proc. U.S. Nat. Mus. 27:657–681.]

———. 1905*a*. A monograph on the isopods of North America. Bull. U.S. Natl. Mus. 54:1–727.

———. 1905*b*. Isopods of the Alaska Salmon Investigation. Bull. U.S. Bur. Fisheries 24:209–221.

———. 1909. Isopods collected in the northwest Pacific by the U.S. Bureau of Fisheries steamer "Albatross" in 1906. Proc. U.S. Nat. Mus. 37: 75–129.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27(2):159–188.

Salemaa, H. 1979. Ecology of *Idotea* spp. (Isopoda) in the northeast Baltic. Ophelia 18:133–150.

Schminke, H. K. 1972. Evolution and homologisierung der mandibeltypen der Bathynellacea (Crustacea, Malacostraca). Zeitschrift f. Zool. Systmatik Evolutionsforshung 10:174–180.

Schram, F. R. 1970. Isopod from the Pennsylvanian of Illinois. Science 169:854–855.

———. 1974. Paleozoic Peracarida of North America. Fieldiana (Geology) 33:95–124.

———. 1978. Arthropods: a convergent phenomenon. Fieldiana (Geology) 39(4):61–108.

———. 1981. On the classification of Eumalacostraca. J. Crustacean Biol. 1(1):1–10.

Schultz, G. A. 1979. Aspects of the evolution and origin of the deep-sea isopod crustaceans. Sarsia 64:77–83.

Shackleton, N. J., and J. P. Kennett. 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279 and 281. Initial Rpts. Deep Sea Drilling Proj. 29:743–756.

Sheppard, E. M. 1957. Isopod Crustacea. Part II. Discovery Rpts. 29:141–198.

Siewing, R. 1958. Anatomie und histologie von *Thermosbaena mirabilis*. Ein beitrag zur phylogenie der reike Pancarida (Thermosbaenacea). Abh. Math.-Naturw. Kl. Akad. Wisk. Mainz 7:197–270.

———. 1963. Studies in malacostracan morphology: results and problems. Pp. 85–103 *in* H. B. Whittington and W. D. I. Rolfe (eds.). Phylogeny and Evolution of Crustacea. Spec. Publ., Mus. Comparative Zool. Harvard Univ. Press, Cambridge.

Simberloff, D., K. L. Heck, E. D. McCoy, and E. F. Conner. 1981. There have been no statistical tests of cladistic biogeographic hypotheses. Pp. 40–63 *in* G. Nelson, and D. E. Rosen (eds.). Vicariance Biogeography: A Critique. Columbia Univ. Press, New York. 593 pp.

Smith, A. G. and J. C. Briden. 1977. Mesozoic and Cenozoic Paleocontinental Maps. Cambridge Univ. Press, London. 63 pp.

Stebbing, T. R. R. 1893. A History of Crustacea. Recent Malacostraca. D. Appleton and Co., New York. 466 pp.

———. 1905. Report on the Isopoda collected by Professor Herdman, at Ceylon, in 1902. Pp. 1–64 *in* W. A. Herdman, Report to the government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar, with supplementary reports upon the marine biology of Ceylon by other naturalists. Part IV, Suppl. Rpt. No. 23. Royal Soc. London.

Steele, D. H. and V. J. Steele. 1975. Egg size and duration of embryonic development in Crustacea. Internat. Revue Ges. Hydrobiol. 60(5): 711–715.

Stock, J. H. 1981. L'origine geologique des Iles des Indes Occidentales en relation avec la dispersion de quelques Malacostraces stygobiontes. Beobios No. 14(2):219–227.

Sywula, T. 1964. A study on the taxonomy, ecology and the geographical distribution of species of genus *Idotea* Fabricius (Isopoda, Crustacea) in Polish Baltic. II. Ecological and zoogeographical part. Bull. Soc. Amis. Sci. Lett. Poznan (D)4:173–199.

Tait, J. 1917. Experiments and observations on Crustacea. Part IV. Some structural features pertaining to *Glyptonotus*. Proc. Roy. Soc. Edinburgh 37:246–303.

Taylor, M. E., and R. M. Forester. 1979. Distributional model for marine isopod crustaceans and its bearing on early Paleozoic paleozoogeography and continental drift. Bull. Geol. Soc. Amer., Pt. 1, 90:405–413.

Wallerstein, B. R., and R. C. Brusca. 1982. Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). J. Biogeography 9:135–150.

Watling, L. 1981. An alternative phylogeny of peracarid crustaceans. J. Crustacean Biol. 1(2): 201–210.

Watrous, L. E. and Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Syst. Zool. 30(1):1–11.

Wiley, E. O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York. 439 pp.

Williams, W. D. 1970. A revision of North American epigean species of *Asellus* (Crustacea: Isopoda). Smithsonian Contrb. Zool. No. 49:1–80.

Woodring, W. P. 1954. Caribbean land and sea through the ages. Bull. Geol. Soc. America 65: 719–732.

———. 1966. The Panama land bridge as a sea barrier. Proc. Amer. Phil. Soc. 110:425–433.

Zinsmeister, W. J. 1974. A new interpretation of thermally anomalous molluscan assemblages of the California Pleistocene. J. Paleontology 48(1):84–94.

———. 1976. Biogeographical significance of the Late Mesozoic and Early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. Pp. 349–355 *in* J. Gray, and A. J. Boucot (eds.). Historical Biogeography, Plate Tectonics, and the Changing Environment. Oregon State Univ. Press, Corvallis. 500 pp.

Note added in proof: Kussakin (1982) recently synonymized west Pacific records of *Cleantioides planicauda* (as *Cleantis planicauda*) with his new *Zenobiana rotunda* Kussakin, 1982. This move restricts the genus *Cleantioides* to the tropical Pacific and Atlantic waters of the New World. (Kussakin, O., 1982, Marine and brackish-water Isopoda of cold and temperate waters of the Northern Hemisphere. II. Anthuridae, Microcerberidae, Valvifera, Tyloidea. [in Russian] Opredeliteli po faune SSSR. Akad. nauk SSSR [Acad. Sci. USSR, Zool.], No. 131.

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Rhamdia reddelli, new species, the first blind pimelodid catfish from Middle America, with a key to the Mexican species

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Abstract. A new blind, depigmented catfish is described and illustrated from Cueva del Nacimiento del Río San Antonio, Oaxaca, México, and compared with its closest relative, *Rhamdia laticauda.* It resembles that species in having strong, retrorse serrae on the pectoral spine, and a shallowly notched caudal fin, but differs in the longer head, longer adipose fin, larger cephalic sensory pores, and longer and more numerous gill rakers (11–16 vs. 9–12). The karyotype (2n = 58) of the new species and a key to described Mexican species are given. A list of nominal and misidentified Mexican species is presented and *R. laticauda, R. parryi,* and *R. guatemalensis* are illustrated.

Resumen. Una nueva especie de bagre anoftalmo y depigmentado de la familia Pimelodidae se describe de la Cueva del Nacimiento del Río San Antonio, Oaxaca, México. Se distingue de *Rhamdia laticauda,* especie estrechamente relacionada a ella, por la cabeza más grande y larga, la aleta adiposa más larga, poros cefálicas más grandes, y por la lóngitud y el número de las branquispinas (11–16 vs. 9–12). El número de las cromosomas (2n = 58), claves para la determinación de los especies de *Rhamdia,* y illustraciones de *R. laticauda, R. parryi,* y *R. guatemalensis* se presentan, y las especies describidas de México se listan.

Heresay reports of blind catfish from Mexico and Central America have persisted since before the turn of the century. As yet, however, the only described eyeless species from this region has been *Prietella phreatophila* Carranza (1954), from northeastern Mexico, a member of the Nearctic family Ictaluridae (6 genera, nearly 40 species). Troglobitic species apparently have evolved at least three times in this family (Lundberg 1982; Reddell 1981:243–244, gives many references to *Prietella*). The Neotropical catfish family Pimelodidae is much larger (about 56 genera and 290 species according to Nelson 1984) but, thus far, only three blind species have been described (see Thines 1955, for references). Two of these are from São Paulo, Brazil (*Pimelodella kronei* and *Caecorhamdella brasiliensis*), the third from Trinidad (*Rhamdia urichi*). A cave population with the eye variably reduced was described recently from Belize as *Rhamdia laticauda typhla* (Greenfield et al. 1983).

For many years it was common practice to assign cavernicolous fishes to distinct genera even though they typically differed from their epigean relatives only in lacking eyes and being depigmented. That viewpoint has changed markedly in recent years (*see* discussions by Roberts and Stewart 1976, and Banister and Bunni 1980) and a number of blind fishes originally placed in monotypic genera have been reassigned to their more widespread surface relatives. In proposing the genus *Caecorhamdia* for *Rhamdia urichi,* Norman (1926) wrote that his genus differed from *Rhamdia* only in lacking eyes and that *C. urichi* was "almost identical" with *Rhamdia quelen,* the type species of *Rhamdia.* Mees (1974:152, 160) agreed, placed *Caecorhamdia* in synonymy with *Rhamdia,* and designated Norman's species as *Rhamdia quelen urichi.* Haseman (1911:325) stated that *Typhlobagrus kronei* is indistinguishable from *Pimelodella lateristrigata,* except for the loss of sight, and recommended that the cave form be relegated to subspecific status.

FIGURE 1. *Rhamdia reddelli*. A, Holotype (♂?), UMMZ 211164, 98.5 mm SL.

Catfishes have anatomical, physiological, and behavioral characteristics that preadapt them to life in darkness (e.g., well developed organs of taste and touch, nocturnal activity, crevice-seeking habits). It is not surprising, therefore, that about 40 percent (17 of 38 species) of the blind fishes that inhabit fresh water are siluroids. Among the five genera of pimelodids inhabiting Middle America, only *Rhamdia* is widely distributed and evolutionarily successful (Bailey and Miller, 1979). The Mexican and Central American representatives of this genus are under review by Reeve M. Bailey and myself; some of our conclusions receive advance notice in this paper.

The eyes of *Rhamdia* are normally small and of secondary importance in their life. Field observations in Honduras by Carr and Giovannoli (1950) of *Rhamdia brachycephala* indicate that this species (a synonym of *R. cabrerai*—*see* below) is "exclusively cavernicolous and thigmotactic" in its swift-water habitat.

The troglobitic species described below differs from its epigean relatives in many features other than depigmentation and loss of eyes. It may be known as:

Rhamdia reddelli new species
Figures 1–3

Synonymy.—*Rhamdia* new species—LeGrande, 1981:42 (chromosome and arm numbers, based on UMMZ 199016). Reddell, 1981:244–245 (mentioned; type locality mapped).

Holotype.—UMMZ 211164, a male? 98.5 mm SL, Cueva del Nacimiento del Río San Antonio, ca. 9 km SW of Acatlán, Oaxaca, on Atlantic slope of eastern Mexico; collected by James R. Reddell and Andy G. Grubbs, 2 January 1977.

Paratypes.—All specimens are from same locality as holotype. UMMZ 199016 (2 specimens: 39 and 70 mm), A. G. Grubbs, M. Cossey, and T. Byrd, 8 January 1976, shipped alive to Ann Arbor (larger individual karyotyped); UMMZ 211165 (6 specimens: 51.5–94.2 mm), taken with the holotype; UMMZ 211166 (77.1 mm), R. Mitchell and L. Faulkenberry, 7 January 1977. AMNH 38216 (98.2 mm), J. Reddell, D. and M. H. McKenzie, S. Murphy, 26 December 1972; AMNH 38217 (4 specimens: 36.7–90.5 mm), same collectors and date; AMNH 38218 (2 specimens: 68.5, 69.5 mm), same collectors, 9 March 1973.

Diagnosis.—A species of *Rhamdia* with a broad, moderately depressed skull in adult, long head, very weak and short occipital process, almost no pigmentation, and lacking eyes (a tiny eye spot occurs in a 37-mm specimen). Related to *R. laticauda* which it resembles in the strong, retrorse serrae on the posterior edge of the pectoral spine and in the shallowly notched caudal fin. From *R. laticauda* and its closest relatives (*see* below) it differs in having: (1) a much longer head and adipose fin, (2) cavernous sensory head pores (especially on chin), and (3) longer and more numerous gill rakers

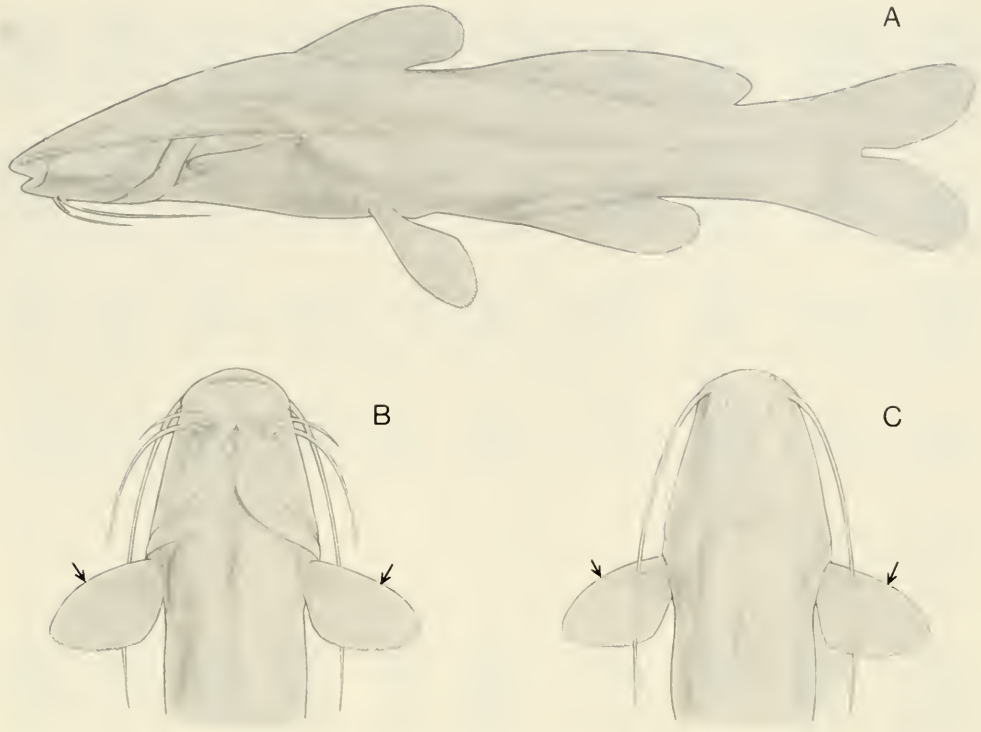

FIGURE 2. *Rhamdia reddelli*. Lateral (A), ventral (B), and dorsal (C) views of paratype, AMNH 38216, 98.2 mm SL. Arrows indicate tips of pectoral spines. The fork of the caudal fin is too deep as drawn.

(11–16 vs. 9–12 on first arch). Head enters SL 3.25–3.75 times (vs. 4.0–5.5) and the depressed dorsal fin overlaps the adipose fin.

Description.—Body form and color pattern are indicated in Figures 1–2. Proportional measurements are presented in Table 1. Meristic data (based on 16 fish) follow. Gill rakers were counted on the first (right) arch, with numbers for upper and lower limbs recorded separately (raker at angle included in lower-limb count). Vertebral counts are post-Weberian, with separation of precaudal and caudal counts where possible (5 vertebrae comprise the Weberian complex). Dorsal fin invariably I,6, the spine soft and flexible as typical of *Rhamdia*; anal rays 13 or 14 (anterior rudiments difficult to see); pectoral rays I,10 or I,11, usually I,10 (22 of 30 counts); pelvic rays invariably 6; principal caudal rays 17–19 (16–18 branched). Gill rakers long, slender, 3+8 to 4+12, total 11(2), 12(0), 13(5), 14(6), 15(1), 16(1). Vertebrae: precaudal, 7 or 8, caudal, 29–32, total 37–39. The number of posterior serrae on the pectoral spine varies with size, from 6–6 in a 36.7-mm SL specimen to 15–14 in a 90.5-mm SL specimen. In the larger fish the serrae are triangular, with very broad bases, and, except proximally, there is no gap between individual serrae as in *Rhamdia laticauda* and closest relatives (*R. parryi, R. salvini, R. cabrerai*[1]). The pectoral spine is gently curved in adults but in specimens less than 70 mm SL it is straight and there are gaps between the individual serrae. There are no serrae on the anterior edge of the spine, which is essentially smooth.

The maxillary barbel is generally longer than in *R. laticauda* and much longer than in *R. parryi, R. salvini,* or *R. cabrerai,* but it is shorter than in *R. guatemalensis* which belongs to a different species group. It may extend backward almost as far as the tip of the depressed dorsal fin and well beyond the origin of the adipose fin, but in some

[1] Meek (1906) named this fish for Señor Cabrera but spelled the patronym *cabrerae*. It is here corrected.

FIGURE 3. Somatic chromosomes at metaphase of female paratype, UMMZ 199016: 2n = 58, FN = 100±4 (LeGrande, 1981:42).

it does not reach beyond the middle of the depressed pectoral fin. The insertion of the pelvic fin lies before the end of the dorsal-fin base. The long adipose fin is well developed, especially posteriorly. The occipital process is very weak and short, extending less than one-fourth the distance to the dorsal-fin origin.

Alive in its natural habitat, *Rhamdia reddelli* is virtually colorless and without visible pigment. In ethyl alcohol (formalin-fixed), the holotype (Fig. 1) has fine, scattered flecks of pigment on the top and sides of the head, along the back and upper sides, and in a narrow band along the lateral line. The lower sides and entire venter are immaculate, as are all the fins except the caudal which has the interradial membranes largely dusky. The similar-sized paratype (Fig. 2) also essentially lacks pigment except for fine flecks along and below the base of the adipose fin and some duskiness on the interradial membranes of the caudal fin. Other adults (between 69 and 91 mm SL), except for one mentioned below, resemble either the holotype or the above-described paratype, or the caudal fin may be immaculate. An 81.5-mm specimen (UMMZ 211165) is more pigmented, with fine flecks extending downward to a line just above the bases of the pectoral, pelvic, and anal fins and with fine pigment grading onto the ventral surface of the caudal peduncle; the venter is otherwise immaculate. Some juveniles (3 or 4 in UMMZ 211165) are pigmented as fully as the holotype, whereas others virtually lack pigment. When kept alive for a month or more in a lighted place, fine melanophores spread over much of the body, covering the venter posterior to the anus and encroaching anteriorly onto the abdomen, with small ones developing along the rays of the paired

TABLE 1. Proportional measurements (in permillage of SL) of 12 specimens (juv.-ad.) of the types of *Rhamdia reddelli*. The data for the holotype are included in the summary. Figures in parentheses are number of specimens when fewer than 12.

Measurement	Holotype	Range	Mean
Standard length, mm	98.5	50.3–98.5	76.8
Body depth	198	163–234	194
Predorsal length	376	366–414	385
Preanal length	682	640–707	675
Anal origin to caudal base	340	300–356	335
Caudal-peduncle length	201	163–206	186
Caudal-peduncle depth	124	99–130	119
Head length	286	278–310	295
Head depth	157	138–171	155
Head width (11)	213	185–226	205
Snout length	123	101–137	120
Mouth width	145	127–151	142
Interorbital width	87	79–100	89
Maxillary-barbel length (9)	434	337–516	466
Outer mental barbel length (11)	211	175–287	229
Inner mental barbel length (11)	128	104–161	127
Adipose-fin length	401	337–417	377
Adipose-fin maximum height	42	29–49	42
Anal-fin basal length	139	131–158	145
Pectoral-fin length (11)	172	157–191	171
Pectoral-spine length	96	91–121	103
Caudal-fin length (9)	211	208–241	223
Caudal fin, to notch (8)	86	76–111	95
Caudal fin, shortest ray length (8)	124	123–149	134

fins and the anal fin as well as on the interradial membranes of the dorsal fin (e.g., the 69-mm SL specimen, UMMZ 199016, kept alive over six months). The one individual with a tiny pigmented pupil (AMNH 38217, 36.7 mm SL) appears to lack pigment.

From the recently described Lake Nicaraguan species *Rhamdia luigiana* Villa (1977), the new species differs markedly in the much deeper body, shorter pectoral spine and fin, longer head, shorter maxillary barbel, shallower caudal-fin notch, and rounded rather than pointed caudal-fin lobes. It also has fewer post-Weberian vertebrae (37–39 vs. 39–42 in *R. luigiana*). *Rhamdia reddelli* is compared with other Mexican species of *Rhamdia* in the Key.

The karyotype (Fig. 3), kindly prepared by William H. LeGrande, shows a diploid number of 58 chromosomes and an arm number (FN) of 100±4. This diploid number may be the ancestral condition for pimelodids, as it evidently is for ictalurids (LeGrande 1981), but since the karyotypes of only seven species of pimelodids have been published (2n = 46, 56, 58, 62—*see* LeGrande 1981:42) this tentative conclusion must await further karyological studies of this family.

Habitat and associates.—The cave is at Cañada San Antonio, approximately 9 km SW of Acatlán, at an elevation of 100 m. The stream flowing from below the cave entrance is the primary source of the Río San Antonio and drains south into Presa Miguel Alemán, a dammed portion of the Río Tonto that is tributary to Río Papaloapan. The main passage of the cave extends for about 120 m to a deep lake containing many blind catfish and crayfish. Beyond this lake a shallow stream extends for 350 m in a passage 10 to 30 m wide and up to 11 m high. Several major side passages that contain secondary streams occur throughout the cave and bring the total length of the cave to about 4.5 km. The main stream floor is generally of sand and gravel with areas of flowstone and bedrock. Both air and water temperatures were 23.5°C. The catfish usually occurred in the deeper ponded portions of the streams, especially in areas over which bats roosted.

A rich invertebrate cave fauna is associated with the catfish. Four species of troglobitic crustaceans inhabit the cave: *Potamalpheops stygicola* Hobbs (Decapoda:

Alpheidae), *Macrobrachium villalobosi* Hobbs (Decapoda: Palaemonidae), *Procambarus (Austrocambarus) oaxacae reddelli* Hobbs (Decapoda: Cambaridae), and *Speleomysis olivae* Bowman (Mysidacea: Lepidomysidae). All have since been collected in other caves in the vicinity of Acatlán. A second species of mysid, *Antromysis (Antromysis) reddelli* Bowman, has been collected from a nearby cave and can be expected to occur in Cueva del Nacimiento del Río San Antonio. A specimen of the alpheid shrimp *Potamalpheops stygicola* was disgorged by a catfish upon preservation. The rarity of shrimps and mysids in pools containing catfish is doubtless related to predation by the fish on the crustaceans. The cave is also inhabited by a possibly troglobitic clam, which is abundant in various parts of the cave but awaits study.

The terrestrial fauna is extremely abundant and includes troglobitic trichoniscid isopods, nicoletiid thysanurans, millipeds, spiders, and opilionids.

Etymology.—I am pleased to name this distinctive species for James R. Reddell, who donated all of the type specimens and has pioneered in exploring caves in Latin America.

Nominal or Misidentified Species Referred to Mexican Catfishes of the Genus *Rhamdia*

Pimelodus laticaudus Heckel in Kner, 1858 (Abtheilung Sitzber. Akad. Wiss. Wien, 26: 420). Type locality (on label in jar): "Rio Xamapa, Mexiko." Oldest available name for a Middle American *Rhamdia*. A valid species. Three syntypes, Vienna Museum 50554 (166, 171, 203 mm SL), examined.

Pimelodus guatemalensis Günther, 1864 (Cat. Fish. British Mus., 5:122). Type locality: Huamuchal, on Pacific coastal plain, Guatemala. A valid species.

Pimelodus godmani Günther, 1864 (ibid.:124). Type locality: Guatemala (Río Motagua, lower Vera Paz) and Mexico. Species illustrated by Regan (Biol. Centrali-Americana, 8:pl. 21, fig. 1). A synonym of *Rhamdia guatemalensis* (Miller 1966:787).

Pimelodus petenensis Günther, 1864 (ibid.:126). Type locality: Lake Petén, Guatemala. Listed for Mexico by Alvarez 1950 (Sec. de Marina, Dir. Gen. Pesca e Ind. Conexas, Mexico:35) with the remark "probably only in Guatemala." Illustrated by Regan (op. cit.:pl. 22, fig. 1). A subspecies of *R. guatemalensis* (Hubbs 1938:266).

Pimelodus hypselurus Günther, 1864 (ibid.:126–127). Type locality (on label in jar): Orizaba [but listed as Cordova in cat. book], Mexico. Holotype, BMNH 1858–11.22.32 (103.5 mm SL), examined by R. M. Bailey; illustrated by Regan (op. cit.: pl. 21, fig. 3). A synonym of *R. laticauda*.

Pimelodus motaguensis Günther, 1864 (ibid.:127). Type locality: Río Motagua, Guatemala. Holotype illustrated by Regan (op. cit.:pl. 20, fig. 1). A synonym of *R. laticauda* (see comment by Miller 1976:4).

Pimelodus brachypterus Cope, 1866 (Trans. Amer. Philos. Soc., 13:404). Type locality: Orizaba, Mexico. Holotype, ANSP 16471 (147 mm SL), examined. A synonym of *R. laticauda*.

Rhamdia parryi Eigenmann and Eigenmann, 1888 (Proc. Calif. Acad. Sci., ser. 2, vol. 1:130). Type locality: Río Zanaleneo [=Sanatenco], near Tonalá, on Pacific slope of Chiapas, Mexico. Five syntypes, MCZ 27273 (77–88 mm SL), examined. A valid species (called *R. hypselura* by Miller 1966:787).

Rhamdia oaxacae Meek, 1902 (Field Col. Mus. Publ. 65:74, pl. 14). Type locality: Río Quiotepec at Cuicatlán, Oaxaca, Mexico, in Río Papaloapan basin. A synonym of *R. guatemalensis* (Regan op. cit.:132).

Rhamdia depressa Barbour and Cole, 1906 (Bull. Mus. Comp. Zool. 50(5):155, pl. 1). Type locality: Ikil [=Ixil] Cenote near Chichén-Itzá, Yucatán, Mexico. A subspecies of *R. guatemalensis* (Hubbs 1936:194).

Rhamdia sacrificii Barbour and Cole, 1906 (ibid.:156). Type locality: Sacrificial cenote near Chichén-Itzá, Yucatán, Mexico. A synonym of *R. guatemalensis* (Hubbs 1936: 200).

Pimelodus boucardi Regan, 1907 (Ann. Mag. Nat. Hist., ser. 7, vol. 19:258). Type

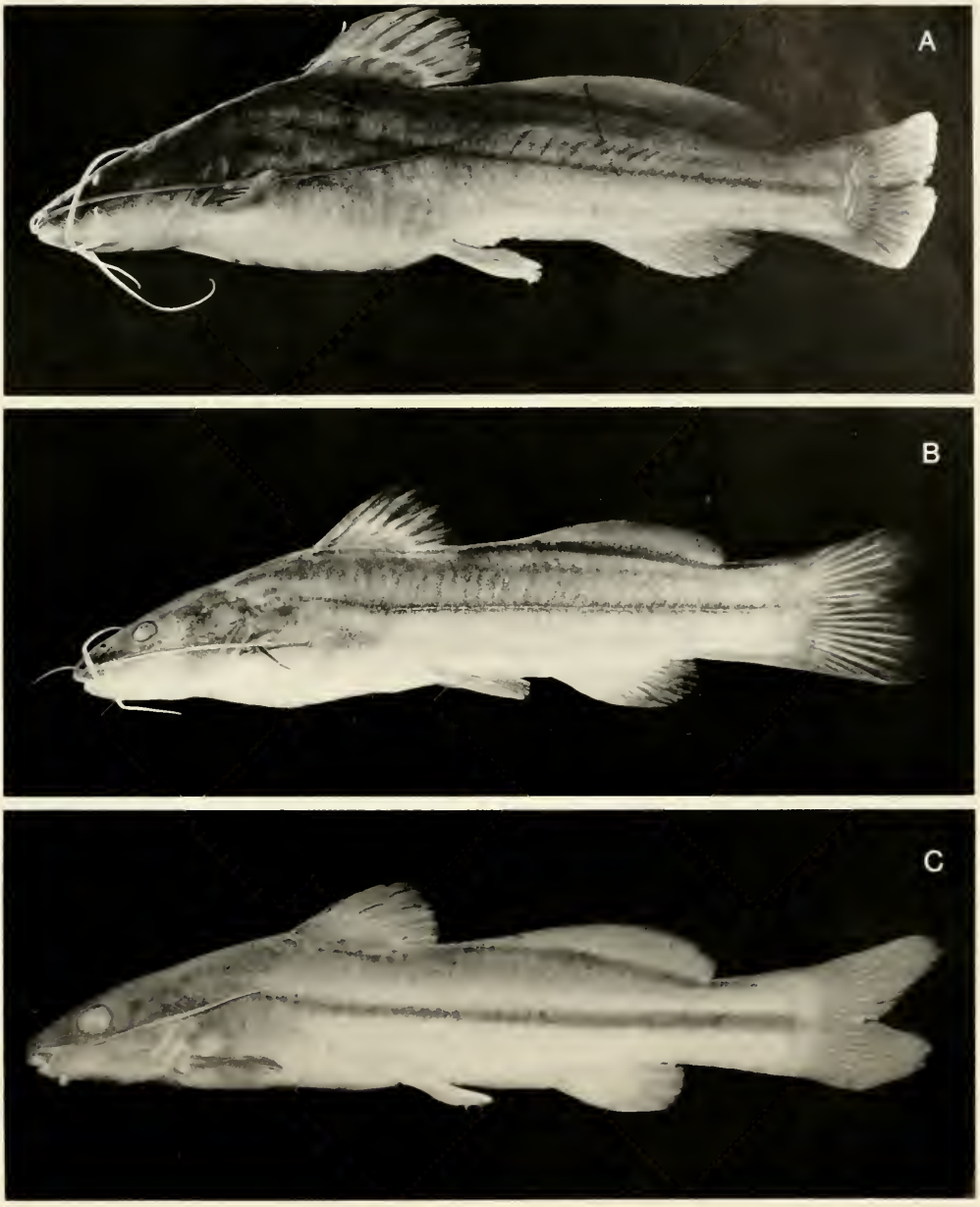

FIGURE 4. Three species of *Rhamdia* from Mexico. A, *R. guatemalensis*, UMMZ 183901 (126.2 mm), Nacimiento del Río Cosalapa, 2.6 km SE of Estación Tezonapa, Veracruz; B, *R. laticauda*, UMMZ 196674 (68.8 mm), tributary to Río Metlac, Fortín, Veracruz; C, *R. parryi*, UMMZ 184739 (68.0 mm), headwaters of Río Tapanatepec, at Hwy 190 bridge E of Tapanatepec, Oaxaca.

locality: Yucatán, Mexico. A synonym of *R. guatemalensis depressa* Barbour and Cole (Hubbs 1936:193, 195); illustrated by Regan (op. cit.:pl. 20, fig. 3).

Pimelodus brachycephalus Regan, 1907 (op. cit.:258). Type locality: Río Nacasil, Pacific slope of Guatemala. Recorded tentatively from Mexico by Alvarez 1950 (op. cit.: 37) with the remark "probably only in Guatemala." Illustrated by Regan (op. cit.: pl. 22, fig. 2). A synonym of *R. cabrerai* (type examined by R. M. Bailey). Later, Alvarez (1970:77) listed *R. brachycephala* from "southeastern Mexico near the

Guatemalan frontier," but this represents a misidentification since *R. cabrerai* is known on the Atlantic slope of Guatemala only from the upper Río Motagua.

Key to Mexican Species of *Rhamdia*[2]

R. laticauda and *R. parryi* are commonly sympatric with *R. guatemalensis.*

1a. Anterior and posterior edges of pectoral spine with small, numerous serrae of subequal length, developed about equally or those on posterior edge somewhat stronger (especially in older fish); caudal fin deeply notched for at least two-thirds the distance from tips of caudal lobes to base of mid-caudal rays. (Maxillary barbel long, typically extending well beyond origin of adipose fin; head long, 3.5–3.8 in SL; adipose fin long, ca. one-third SL; occipital process long, extending nearly half way or more to dorsal origin.) *Atlantic and Pacific lowlands from just NW of Veracruz City on Atlantic slope and Rio Tehuantepec basin on Pacific versant southward to Panama* (if *R. wagneri* is a synonym—*see* Hubbs 1936:181); typically in pools ..... *Rhamdia guatemalensis* (Fig. 4)

b. Pectoral spine with strong, retrorse to nearly straight serrae only on posterior edge (anterior edge smooth or roughened); caudal fin weakly notched, to no more than half distance from tips of caudal lobes to base of mid-caudal rays. *Atlantic and Pacific versants*; cavernicolous and in rocky streams of piedmont slopes and foothills 2

2a. Skull depressed; head long, 3.25–3.75 in SL; blind and depigmented; adipose fin well developed, overlapped by depressed dorsal fin. *Cueva del Nacimiento del Río San Antonio, Oaxaca*; cavernicolous ..... *Rhamdia reddelli* (Figs. 1–2)

b. Skull domed; head short, 4.0–5.5 in SL; eyes and pigment well developed; adipose fin short, not (or rarely) overlapped by depressed dorsal fin 3

3a. A prominent, dark lateral stripe on midside, from behind head to base of caudal fin, becoming broader posteriorly; post-Weberian vertebrae fewer, 35–38, usually 36 or 37 (98%). *Pacific slope of Oaxaca and Chiapas southeastward into Guatemala (to Dpto. de Santa Rosa)*; on rocky riffles ..... *Rhamdia parryi* (Fig. 4)

b. Side of body without a conspicuous dark stripe; post-Weberian vertebrae more numerous, 37–41, usually 38–40 (91%). *Atlantic slope from Río Jamapa, Veracruz, southeastward to western Honduras*; on rocky riffles and in current of streams ..... *Rhamdia laticauda* (Fig. 4)

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[2] Much of this key was derived from information provided by R. M. Bailey.

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Literature Cited

Alvarez, J. 1970. Peces mexicanos (claves). Inst. Nac. Inv. Biol. Pesq., Ser. Inv. Pesq., Estudio No. 1, México. 166 pp.

Bailey, R. M., and R. R. Miller. 1979. Pimelodid catfishes (genus *Rhamdia*) from northern Middle America. Abst. 59th Ann. Mtg. Amer. Soc. Ich. & Herp., Orono, Maine. 1 p.

Banister, K. E., and M. K. Bunni. 1980. A new blind cyprinid fish from Iraq. Bull. Brit. Mus. Nat. Hist. (Zool.) 38(3):151–158.

Carr, A. F. Jr., and L. Giovannoli. 1950. The fishes of the Choluteca drainage of southern Honduras. Occ. Pap. Mus. Zool. Univ. Mich. 523:1–38.

Carranza, J. 1954. Descripción del primer bagre anoftalmo y depigmentado encontrado en aguas mexicanas. Ciencia 14(7–8):129–136.

Greenfield, D. W., T. A. Greenfield, and R. L. Woods. 1983. A new subspecies of cave-dwelling pimelodid catfish, *Rhamdia laticauda typhla*, from Belize, Central America. Brenesia 19/20(1982):563–576.

Haseman, J. D. 1911. Descriptions of some new species of fishes and miscellaneous notes on others obtained during the expedition of the Carnegie Museum to central South America. Ann. Carnegie Mus. 7(3–4):315–328.

Hubbs, C. L. 1936. Fishes of the Yucatan Peninsula. Carnegie Inst. Wash. Publ. 457:157–287.

———. 1938. Fishes from the caves of Yucatan. Carnegie Inst. Wash. Publ. 491:261–295.

LeGrande, W. H. 1981. Chromosomal evolution in North American catfishes (Siluriformes: Ictaluridae) with particular emphasis on the madtoms, *Noturus*. Copeia 1981(1):33–52.

Lundberg, J. G. 1982. The comparative anatomy of the toothless blindcat, *Trogloglanis pattersoni* Eigenmann, with a phylogenetic analysis of the ictalurid catfishes. Misc. Publ. Mus. Zool. Univ. Mich. 163:1–85.

Meek, S. E. 1906. Description of three new species of fishes from Middle America. Field Col. Mus. Publ. 116, Zool. Ser. 7(3):93–95.

Mees, G. F. 1974. The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi). Zoolog. Verhand. 132:1–256 + pls. 1–15.

Miller, R. R. 1966. Geographical distribution of Central American freshwater fishes. Copeia 1966(4):773–802.

———. 1976. An evaluation of Seth E. Meek's contributions to Mexican ichthyology. Fieldiana, Zool. 69(1):1–31.

Nelson, J. S. 1984. Fishes of the World. 2nd ed. John Wiley & Sons, N. Y. 416 pp.

Norman, J. R. 1926. A new blind catfish from Trinidad, with a list of the blind cave-fishes. Ann. Mag. Nat. Hist. ser. 9, vol. 18:324–331.

Reddell, J. R. 1981. A review of the cavernicole fauna of Mexico, Guatemala, and Belize. Texas Mem. Mus., Bull. 27:1–327.

Roberts, T. R., and D. J. Stewart. 1976. An ecological and systematic survey of fishes in the rapids of the lower Zaire or Congo River. Bull. Mus. Comp. Zool., Harvard Univ. 147(6):239–317.

Thines, G. 1955. Les Poissons aveugles (1): origine, taxonomie, répartition, géographique, comportement. Ann. Soc. Roy. Zool. Belgique 86(1):5–128.

Villa, J. 1977. A new species of pimelodid catfish of the genus *Rhamdia* from Nicaragua, Central America. Brenesia 12/13:133–142.

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A complete specimen of *Peachella brevispina* Palmer—an unusual olenellid trilobite (Arthropoda: Olenellida) from the lower Cambrian of California

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Abstract. The thorax and possible pygidium of *Peachella brevispina* are described for the first time from a recently collected complete specimen, the first recovered for this genus. Unusual features include the large macropleural third segment of the prothorax that distorts the adjacent pleurae, the rounded distal extremeties of the other prothoracic segments, the rather gradual transition from the prothorax to the opisthothorax, and the large, triangular pygidium.

Introduction

Olenellid trilobites are found in Lower Cambrian strata in various parts of the world, and numerous specimens have been collected from localities in western North America. Olenellids are broad, flat, medium to large-sized trilobites characterized by a large semicircular cephalon, prominent ocular lobes, numerous thoracic segments that terminate laterally in spines of various lengths, and a small pygidium. The absence of specialized morphologic features on the thorax that were used for enrollment in other trilobites (Bergström 1973:17) indicates that trilobites of the Family Olenellidae were unable to enroll (Harrington 1959:102), a protective feature that developed in other Lower Cambrian (Rasetti 1948:17–18, pl. 4, figs. 22–24) and later trilobites.

Initial taxonomic efforts on olenellid trilobites resulted in the recognition of a number of closely related genera (Walcott 1910) and species (Resser and Howell 1938). More recent work (Fritz 1972, Palmer and Halley 1979) has resulted in recognition of fewer genera, because the criteria originally used to discriminate certain genera intergrade among various species. Added to this problem is the fact that olenellids frequently occur in the same beds of rock in pairs of closely related taxa that have been variously interpreted as paired species or dimorphs (see Palmer and Halley 1974:66–67 for a recent discussion of these taxonomic problems).

The complete specimen of *Peachella brevispina* Palmer described in this paper was collected by R. L. Clark from the lower part of the Carrara Formation at Emigrant Pass in the Nopah Range, Inyo County, California (Fig. 1). Palmer and Halley (1979: 13, 75; fig. 1) reported that *P. brevispina* is moderately rare in the Thimble Limestone Member of the Carrara in the nearby Dublin Hills and at Eagle Mountain. Mount (1980:78–80; fig. 1) described the Emigrant Pass locality in the Nopah Range, including a detailed columnar section and range chart in which he reported *P. brevispina* from a thin limestone bed near the top of an unnamed lower member of the Carrara. Mount's columnar section supports Palmer and Halley's observation (p. 9, 13; figs. 6A, 11) that the Thimble Limestone Member of the Carrara cannot be recognized in the Nopah Range because the Thimble grades southeastward into shale.

Peachella is an unusual genus of olenellid trilobites that was known only from a small number of cephala before Clark's discovery of the complete specimen described in this paper. The glabella, ocular lobes and cephalic border are fainter and less well defined than usual for an olenellid. The most unusual feature of the cephalon is the genal spines, which are normally long and pointed in other olenellids but in species of *Peachella* are short, wide and have broadly rounded tips. First described by Walcott in 1910, this scarce genus included only the type species *Peachella iddingsi* (Walcott) until 1979, when Palmer described a second species, *P. brevispina,* from the Thimble Limestone. Clark's discovery of a complete specimen, which he donated to the San Diego Natural History Museum (SDSNH locality no. 3169), allows the description of this unusual trilobite to be completed.

Morphologic terms used in the following description are defined in Harrington (1959). Suprageneric classification follows Bergström (1973) and Palmer and Halley (1979).

Systematic Paleontology

Phylum Arthropoda Siebold and Stannius, 1845
Class Trilobita Walch, 1771
Order Olenellida Resser, 1938
Family Olenellidae Vogdes, 1893
Genus *Peachella* Walcott, 1910
Peachella brevispina Palmer, 1979
Figures 2, 3

Peachella brevispina PALMER *in* Palmer and Halley (1979:75, pl. 5, figs 1–3).

Material.—1 complete decalcified specimen (SDSNH 24548) preserved as internal and external molds; specimen slightly deformed, especially the cephalon and pygidium.

Description.—Length of specimen 33 mm (excluding macropleural spines). Cephalon semicircular in outline with short, paddle-like genal spines. Anterior end of cephalon poorly preserved. Glabella prominent, elongate, extends close to anterior edge of cephalon, set off by rather shallow axial furrows. No lateral glabellar or occipital furrows visible. Occipital ring not differentiated. Ocular lobes poorly preserved, apparently short, arcuate and located close to the glabella. Anterior border and border furrow not preserved. Lateral border narrow opposite anterior end of glabella, gradually widens posteriorly. Lateral border furrow shallow, curved slightly adaxially at anterior end of genal spine, crossing adaxial base of genal spine and continuing to posterior margin of cephalon. Posterior border furrow not visible. Characteristic genal spines short, broad, moderately inflated, posterolaterally directed; spine termination broadly rounded.

Prothorax of 15 segments. Axis prominent, convex, width (trans.) approximately one-fourth of prothoracic width. Most articulating half-rings visible on outstretched specimen. Axial furrows shallow. Axial ring and transverse furrow of first prothoracic segment slope steeply anteriorly, articulating half-ring apparently still connected to posterior ventral edge of cephalon. Axial ring of second prothoracic segment separated from narrow articulating half-ring by prominent, wide, deep transverse furrow that curves slightly anteriorly abaxially and intersects the axial furrows. Remaining axial rings separated from articulating half-rings by faint, narrow transverse furrow that curves anteriorly abaxially and terminates near anterior edge of ring before reaching axial furrows. This furrow deepest on axial rings of prothoracic segments 12–14, becoming progressively fainter on anterior segments. Small axial node present on posterior edge of axial rings of prothoracic segments 10–14; node most prominent on segment 14, progressively diminishing in size anteriorly. Prothoracic segment 15 broken at axis, undoubtedly bears axial spine whose mold can be seen entering the surrounding rock just posterior of the opisthothorax.

Pleurae of prothorax variable in appearance. Pleurae of first two prothoracic seg-

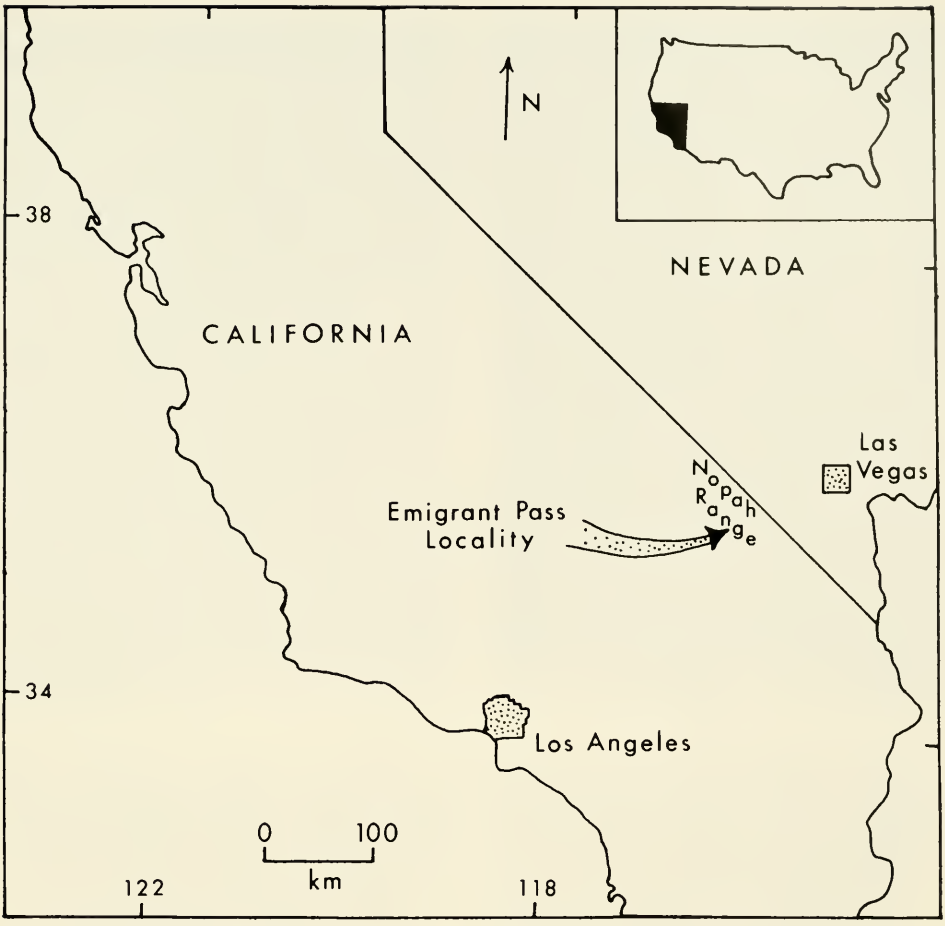

FIGURE 1. Map showing location of Emigrant Pass locality where described specimen was collected.

ments not well preserved, appearing flat with no pleural furrows and rounded distal extremities. Faint transverse ridge(s) present on left pleurae of segments 1 and 2 not present on right pleurae, and interpreted to be result of deformation of specimen. Pleurae of segment 3 expand rapidly abaxially, especially along posterior edge, becoming broadly oval in shape and approximately seven times as long (exsag.) as the pleurae of any other segment. Pleurae of segment 3 reach maximum length (exsag.) near distal margins of thorax, pleurae narrow abaxial of maximum length to form large, long macropleural spine that curves posteriorly and extends well beyond the posterior end of the specimen. Unusual ovoid shape of pleurae of segment 3 distorts shape of pleurae of segments 2 and 4–6, forcing these pleurae to compress abaxially and to taper distally (to rounded extremeties) in order to accommodate wider pleurae of segment 3 without leaving gaps or overlaps between pleurae. Pleurae of prothoracic segments 7–14 rather plain, nearly flat, with rounded distal extremeties. All pleurae posterior of third pleurae divided into narrow anterior and posterior bands by broad, shallow pleural furrow. Pleural furrow narrower and deeper in segments 12–14. Pleurae of prothoracic segments 10–14 bend gently to the posterior abaxially, with posterior bending greatest toward posterior end of prothorax.

Opisthothorax consists of eight or nine segments. Axis only faintly defined by very shallow axial furrows. Pleurae simple, nearly flat, apparently with no pleural furrows and rounded distal extremeties.

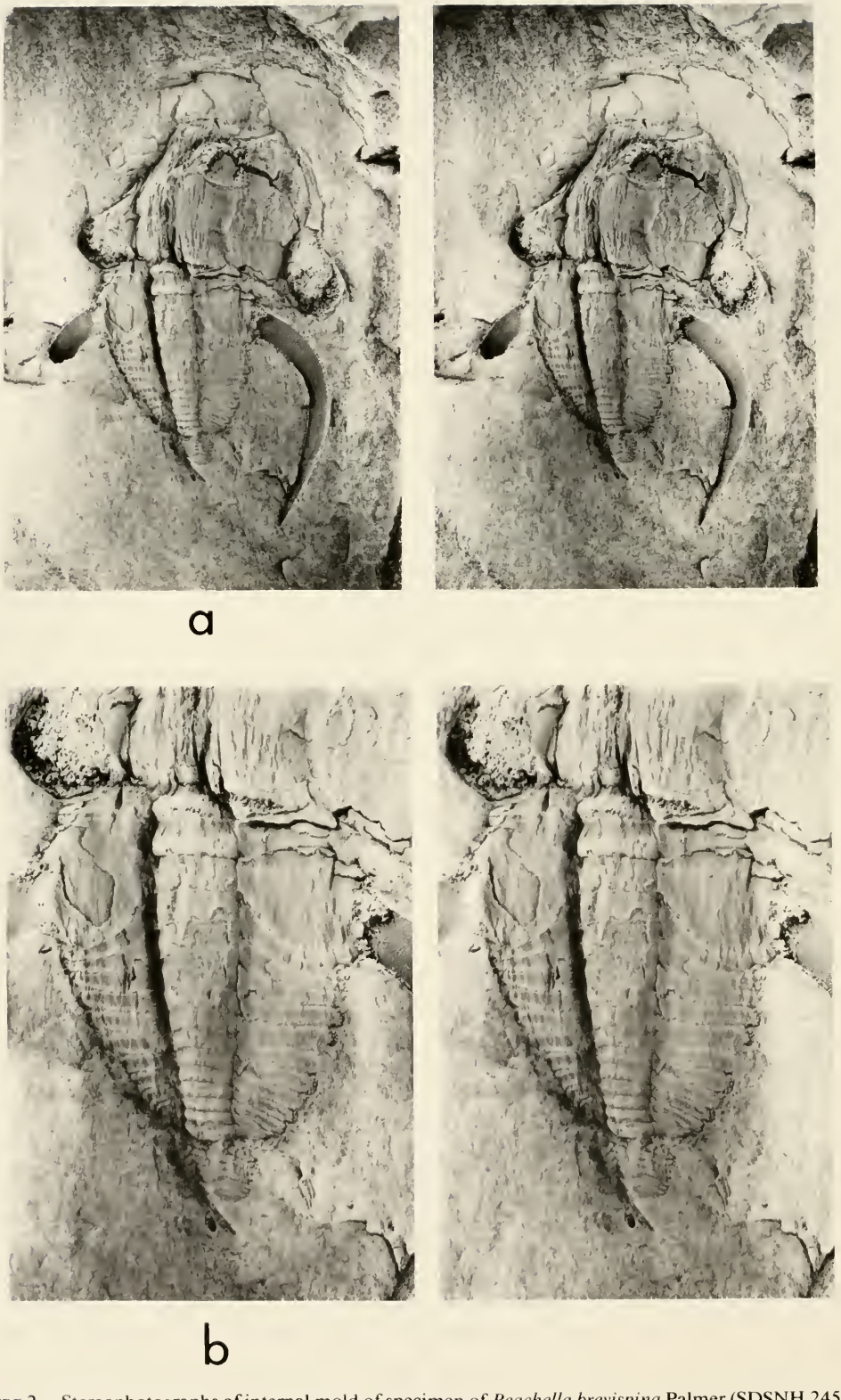

FIGURE 2. Stereophotographs of internal mold of specimen of *Peachella brevispina* Palmer (SDSNH 24548) from lower part of Carrara Formation, Emigrant Pass, California; a. entire specimen, ×2; b. enlargement of thorax and pygidium, ×4.

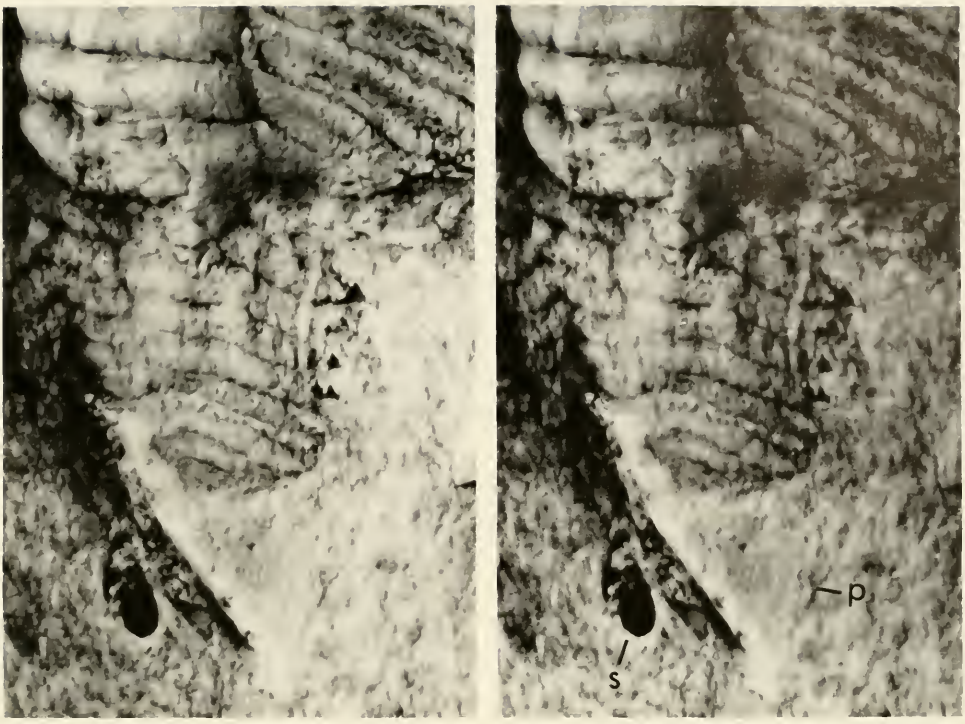

FIGURE 3. Stereophotographs (×16) of segments 13–15 of the prothorax, the opisthothorax, and the possible pygidium (p) of *Peachella brevispina* Palmer. The pygidium is poorly preserved and twisted underneath and to the right so that only the axis and right pleural region are visible. Note also that the axial ring of prothoracic segment 15 is broken. The base of the spine that extended upward and backward from this segment is preserved on the counterpart to this specimen, and the mold of this spine (s) enters the rock to the left of the possible pygidium.

Pygidium possibly present, although twisted to right and only partly preserved on internal and external molds. Overall shape broadly triangular, with convex axis tapering posteriorly and extending almost to pygidial margin. Pleural area smooth, slightly convex, with no border or border furrow.

Remarks.—The cephalon of *Peachella brevispina* is characterized by its faintly defined glabella and border furrow, short ocular lobes, and short, moderately inflated paddle-like genal spines. The cephala illustrated by Palmer and Halley (1979, pl. 5, figs. 1, 2) are much better preserved than the cephalon on this complete specimen.

The most unusual features of the prothorax are the pleurae of the third segment, which expand rapidly away from the axial furrows and become broadly oval in shape, crowding and distorting the adjacent pleurae. Other unusual features include the rounded distal extremeties of the prothoracic pleurae; on most olenellid trilobites, the pleurae terminate laterally in spines. The prothoracic segments diminish in size posteriorly and somewhat grade into the segments of the opisthothorax, although the junction between these two parts of the thorax is not perfectly preserved. Palmer (in Palmer and Halley 1979:73) described a partly preserved thorax of *Olenellus multinodus* (pl. 4, figs. 7, 8) that has enlarged pleurae on the third prothoracic segment and a gradual transition from the pleurae of the prothorax to the pleurae of the opisthothorax. He suggests that these features might merit placing *O. multinodus* in a new genus (possibly with *Olenellus arcuatus*) if additional specimens prove that these features are characteristic of the species. These two species also have short ocular lobes. Similar features are present on *P. brevispina,* which has in addition the unusual and generically distinctive paddle-shaped genal spines not present on *O. multinodus* or *O. arcuatus.* This mix of similar

unusual features on species that clearly belong in different genera illustrates once again some of the problems in generic level taxonomy in olenellids.

If indeed the pygidium of *P. brevispina* is preserved in a twisted position at the posterior end of the opisthothorax, then *P. brevispina* also has an unusual pygidium for an olenellid to add to its other peculiarities. Olenellid pygidia (when preserved) are very small, short trapezoidal plates attached to the end of the narrow opisthothorax. The apparent pygidium of *P. brevispina* is relatively large, triangular in shape, and has broad, smooth pleural areas, a combination which makes the pygidium of this species unique among olenellids.

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Literature Cited

Bergström, Jan. 1973. Organization, life, and systematics of trilobites. Fossils and Strata 2:1–69.

Fritz, W. H. 1972. Lower Cambrian trilobites from the Sekwi Formation type section. Canadian Geological Survey Bulletin 212.

Harrington, H. J. 1959. General description of Trilobita, p. 38–126 *in* R. C. Moore (ed.). Treatise on Invertebrate Paleontology, Part 0, Arthropoda 1. Geological Society of America and the University of Kansas Press, Lawrence, Kansas.

Mount, J. D. 1980. An Early Cambrian fauna from the Carrara Formation, Emigrant Pass, Nopah Range, Inyo County, California: a preliminary note, p. 78–80 *in* Paleontological Tour of the Mojave Desert, California-Nevada. Southern California Paleontological Society Special Publication No. 2.

Rasetti, Franco. 1948. Lower Cambrian trilobites from the conglomerates of Quebec. Journal of Paleontology 22:1–24.

Resser, C. E., and B. F. Howell. 1938. Lower Cambrian *Olenellus* Zone of the Appalachians. Geological Society of America Bulletin 49:195–248.

Palmer, A. R., and R. B. Halley. 1979. Physical stratigraphy and trilobite biostratigraphy of the Carrara Formation (Lower and Middle Cambrian) in the southern Great Basin. United States Geological Survey Professional Paper 1047.

Walcott, C. D. 1910. *Olenellus* and other genera of the Mesonacidae. Smithsonian Miscellaneous Collections 53:233–422.

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Type specimens of amphibians and reptiles in the San Diego Natural History Museum

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Publishing a list of type specimens in a collection serves several purposes. For those who compile them, the inventory is a propitious means of revealing the taxonomic and nomenclatural errors and inconsistencies that routinely creep into a collection. For users, the list provides a comprehensive reference to that institution's holdings of primary and secondary types, and serves as a guide to the original literature, perhaps even yielding insights into the nomenclatural history of the taxa.

In generating the present account, we made use of the only previous publication of type specimens of amphibians and reptiles in the San Diego Natural History Museum, compiled by Allan J. Sloan in 1965 (Transactions San Diego Society of Natural History (14(1):1–8). Sloan listed only holotypes, which at the time numbered 48, all of reptiles. To make the present list more comprehensive we have included all paratypic material, and revised the now expanded list of holotypes.

The collection currently includes holotypes of 1 frog, 14 lizards and 41 snakes. As well, there are several hundred paratypes of 24 additional taxa. Locating all secondary types in the collection was a difficult task because many of these specimens had not been so designated in the early years of cataloging, nor were they segregated from the main collection. Subspecies comprise the majority of primary and secondary types, many of which have been synonymized since their original description. Readers familiar with the collections of amphibians and reptiles at the San Diego Natural History Museum are aware that the geographic emphasis favors the Southwest, Baja California and the Gulf of California Islands; this is reflected in the type localities that follow.

For many years the collections of amphibians and reptiles at the San Diego Natural History Museum were closely tied to the activities of Laurence M. Klauber, although the full history extends beyond the Klauber era back to the Society's inception in 1874. Klauber began his herpetological studies as an avocation in 1920, conducting most of his research and maintaining the collections in the basement of his home. By 1960 he had amassed 35 000 specimens. These, as well as his vast library of over 20 000 books and reprints, were donated to the San Diego Society of Natural History, whence they were housed in the Natural History Museum in Balboa Park. At the time of Klauber's death in 1968, the number of specimens of amphibians and reptiles at the museum was over 50 000.

Over the years the collection has had many contributors, among the earliest being the celebrated naturalists of the Southwest, Charles R. Orcutt and Frank Stephens. Later, during the middle third of this century, the collection benefited considerably from the efforts of C. B. Perkins and Charles E. Shaw. Klauber's legendary interest in rattlesnakes alone resulted in an enormous series of *Crotalus* and a substantial representation of reptiles native to the Far West and northern Mexico. Indeed, during the 110-year history of the Society, the museum has benefited from the interests and travels of many individuals. Hence, the collections of amphibians and reptiles are flavored

with series of taxa from, for example, the Galápagos Islands, the Pacific, and the Caribbean.

As early as 1928, Klauber foresaw that someday his collection and that of the museum would merge, and he assigned specimen numbers accordingly so that they would not have to be recatalogued at a future date. Consequently, all specimens originally in the LMK series have the same numbers in the herpetological catalogue of the San Diego Natural History Museum. The collection now has approximately 65 000 specimens which may be broken down taxonomically as follows:

Amphibians (Apoda, Caudata, Anura)—18 families, 60 genera, 175 species
Turtles—9 families, 34 genera, 80 species
Lizards (including amphisbaenians and *Sphenodon*)—17 families, 130 genera, 360 species
Snakes—9 families, 195 genera, 400 species

These taxa also encompass nearly 2000 skeletons in roughly the same diversity, and several hundred preserved hemipenes representing 70 species of snakes (mostly *Crotalus*) and lizards.

About This List

Each species entry begins with the author, date and publication of the original description; the specific page number where the description appears is given parenthetically at the end of that citation. This line is followed by the SDSNH number of the holotype, sex, type locality and the name of the collector and date that the specimen was caught. In nearly all instances, we have tried to preserve the original wording for the type locality. Where potential confusion exists because of orthography or archaic and vague place names, we have clarified them as needed, inside brackets [ ] or at the bottom of the entry under *Remarks*. When only the paratype(s) of a taxon is represented in the SDSNH collection, the holotype and catalogue number of the holding institution is given under *Remarks*.

Each taxon is listed alphabetically by genus, species and subspecies precisely as it was originally designated, that is, irrespective of present usage. For those taxa that have been synonymized or whose nomenclature is currently in doubt, this is so noted under *Remarks* with the name and publication of the first authority or revisor. We have made no nomenclatural decisions per se, and a particular taxon is considered valid unless indicated.

Abbreviations of museums and personal collections are as follows:

AMNH: American Museum of Natural History
BYU: Brigham Young University
CAS: California Academy of Sciences
CAS—SU: California Academy of Sciences—Stanford University collection
CM: Carnegie Museum
EHT: Edward H. Taylor collection*
FMNH: Field Museum of Natural History
LACM: Los Angeles County Natural History Museum
MCZ: Museum of Comparative Zoology, Harvard University
SDSNH: San Diego Society of Natural History
SU: Stanford University Natural History Museum*
T-S: Edward H. Taylor and Hobart M. Smith, University of Kansas*
UIMNH: University of Illinois, Museum of Natural History
UMMZ: University of Michigan, Museum of Zoology
USNM: National Museum of Natural History

* Specimens from these collections have been dispersed to other institutions.

ANURA

Bufo exsul Myers (1942)
Occ. Papers Mus. Zool. Univ. Michigan 460:1–13 (p. 3).

Paratypes.—SDSNH 29098 and 29099 Deep Springs, Inyo Co., California.
Remarks.—=*Bufo boreas exsul* according to Stebbins (1962, Amphibians of Western North America. Univ. Calif. Press). Holotype: UMMZ 83357 a very large female.

Hyla regilla cascadae Jameson, Mackay and Richmond (1966)
Proc. California Acad. Sci. 4th ser. 33(19):551–620 (p. 602).

Paratypes.—SDSNH 44971–44987 ½ mi S of Bend, Deschutes Co., Oregon.
Remarks.—Holotype: CAS 101038 an adult male.

Hyla regilla deserticola Jameson, Mackey and Richmond (1966)
Proc. California Acad. Sci. 4th ser. 33(19):551–620 (p. 582).

Holotype.—SDSNH 54176 an adult male; San Borjas, Baja California Norte, Mexico. By David L. Jameson, November 25, 1961.
Paratypes.—SDSNH 54166–54175 data same as for Holotype.
Remarks.—=*Hyla regilla hypochondriaca* according to Duellman (1970, Univ. Kansas Mus. Nat. Hist. Monog. No. 1:487). San Borjas reads San Borja on recent maps.

Hyla regilla pacifica Jameson, Mackey and Richmond (1966)
Proc. California Acad. Sci. 4th ser. 33(19):551–620 (p. 591).

Paratypes.—SDSNH 53514–53529 4 mi S of Waldport, Lincoln Co., Oregon.
Remarks.—Holotype: CAS 101007 an adult male.

Hyla regilla palouse Jameson, Mackey and Richmond (1966)
Proc. California Acad. Sci. 4th ser. 33(19):551–620 (p. 599).

Paratypes.—SDSNH 44715–44718 6 mi SE of La Grande, Union Co., Oregon.
Remarks.—Holotype: CAS 100982 an adult male.

Hyla regilla sierrae Jameson, Mackey and Richmond (1966)
Proc. California Acad. Sci. 4th ser. 33(19):551–620 (p. 605).

Paratypes.—SDSNH 53835–53841 1¼ mi SSE of Tioga Pass Ranger Station, E entrance to Yosemite National Park, Mariposa Co., California.
Remarks.—Holotype: CAS 100991 an adult male.

SAURIA

Anniella geronimensis Shaw (1940)
Trans. San Diego Soc. Nat. Hist. 9(24):225–228 (p. 225).

Holotype.—SDSNH 7543 an adult female; San Geronimo Island, Lower California [Norte], Mexico. By Margaret [Mrs. Griffing] Bancroft, March 28, 1932.
Paratypes.—SDSNH 7542 data same as for Holotype.
Remarks.—=*Anniella pulchra* according to Hunt (1983, Copeia (1):79–89).

Anolis rivalis Williams (1984)
Breviora 478:1–22 (p. 7).

Paratype.—SDSNH 31163 "Port Utria," [south of Punta Solano, Chocó] Colombia.
Remarks.—Holotype: LACM 42124 an adult male.

Coleonyx variegatus abbotti Klauber (1945)
Trans. San Diego Soc. Nat. Hist. 10(11):133–216 (p. 154).

Holotype.—SDSNH 34790 an adult male; Proctor Valley, San Diego Co., California. By William Moore, February 28, 1942.
Paratypes.—As follows: California: Los Angeles Co.: SDSNH 2011 San Francisquito Plant 2. Riverside Co.: SDSNH 2725 Moreno. San Diego Co.: SDSNH 30 Cot-

tonwood; SDSNH 843 Foster; SDSNH 16702 Rincon; SDSNH 16988, 32817, 34786 Mission Gorge; SDSNH 16989 Jamul; SDSNH 17012 De Luz (says "Sentenac Canyon" in catalogue); SDSNH 21249 El Capitan; SDSNH 24050 San Pasqual; SDSNH 25303, 34666 Jacumba; SDSNH 27770 Foot Agua Tibia Mt.; SDSNH 32797 Pala; SDSNH 32821–32822 Black Mtn. near La Mesa. Baja California Norte, Mexico: SDSNH 2593 Ensenada; SDSNH 5265–5266, 15970–15971, 27726, 30295 Cedros Island; SDSNH 6553 65 mi SE of Tecate; SDSNH 24390 San José (lat. 32°).

Coleonyx variegatus bogerti Klauber (1943)
Trans. San Diego Soc. Nat. Hist. 10(11):133–216 (p. 176).

Holotype.—SDSNH 32486 an adult male; Xavier, Pima Co., Arizona. By Lee W. Arnold, July 17, 1939.
Paratypes.—None designated.

Coleonyx variegatus utahensis Klauber (1943)
Trans. San Diego Soc. Nat. Hist. 10(11):133–216 (p. 171).

Holotype.—SDSNH 35792 an adult male; Watercress Spring, Washington Co., Utah. By Dr. Ross Hardy, April 16, 1941.
Paratypes.—SDSNH 36021–36024 data same as for Holotype.

Phyllodactylus angelensis Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 444).

Holotype.—SDSNH 19996 an adult male; north end of Isla Angel de la Guarda, Baja California [Norte], Mexico. By Allan J. Sloan, March 22, 1963.
Paratype.—SDSNH 50851 Isla Pond, [Baja California Norte, Mexico].

Phyllodactylus apricus Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 450).

Holotype.—SDSNH 44623 an adult male; Isla Las Animas, Baja California [Sur, Mexico]. By Chris Parrish and G. E. Lindsay, June 27, 1964.
Paratypes.—SDSNH 44620–44622, 44624, 50830–50842, 50844–50849 data same as for Holotype.

Phyllodactylus bugastrolepis Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 447).

Paratypes.—SDSNH 44604–44607, 44611–44613, 50792, 50793 Isla Catalina, Baja California [Sur, Mexico].
Remarks.—Holotype: CAS 98485 an adult female.

Phyllodactylus homolepidurus nolascoensis Dixon (1964)
New Mexico State Univ. Sci. Bull. 64(1):1–139 (p. 42).

Paratypes.—SDSNH 6840 and 6841 Isla San Pedro Nolasco, Sonora, Mexico.
Remarks.—Holotype: CAS 50552 an adult male.

Phyllodactylus partitus Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 445).

Paratypes.—SDSNH 6834–6836, 39258, 39649, 40508, 50820–50822 Isla Partida (N), Baja California [Norte, Mexico].
Remarks.—Holotype: CAS 98429 an adult male.

Phyllodactylus santacruzensis Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 449).

Paratypes.—SDSNH 50872, 50873 Isla Santa Cruz, Baja California [Sur, Mexico].
Remarks.—Holotype: CAS 98468 an adult female.

Phyllodactylus xanti acorius Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 442).

Paratypes.—SDSNH 50827–50829 Isla San Diego, Baja California [Sur, Mexico].

Remarks.—=*Phyllodactylus nocticolus acorius* according to Murphy (1983, Occ. Papers California Acad. Sci. 137:1–48). Holotype: CAS 98451 an adult male.

Phyllodactylus xanti angulus Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 433).

Paratypes.—SDSNH 44677, 44678, 50868, 50869 Isla Salsipuedes, Baja California [Norte, Mexico]; SDSNH 44238, 44239, 50833, 50856–50859 [Isla] San Lorenzo, [Baja California Norte, Mexico].

Remarks.—=*Phyllodactylus nocticolus angulus* according to Murphy (1983, Occ. Papers California Acad. Sci. 137:1–48). Holotype: CAS 98477 an adult male.

Phyllodactylus xanti circus Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 439).

Holotype.—SDSNH 50814 an adult female; Isla Ildefonso [Baja California Sur, Mexico]. By Charles E. Shaw, April 2, 1962.

Paratypes.—SDSNH 50809–50812, 50815–50817 data same as for Holotype.

Remarks.—=*Phyllodactylus nocticolus circus* according to Murphy (1983, Occ. Papers California Acad. Sci. 137:1–48).

Phyllodactylus xanti estebanensis Dixon (1966)
Proc. California Acad. Sci. 4th ser. 33(13):415–452 (p. 437).

Paratypes.—SDSNH 50852 and 50853 Isla Tiburon [Gulf of California, Mexico]; 50870 and 50871 Isla San Estéban [Gulf of California, Mexico].

Remarks.—=*Phyllodactylus nocticolus estebanensis* according to Murphy (1983, Occ. Papers California Acad. Sci. 137:1–48). Holotype: CAS 98481 an adult male. Isla Tiburon and Isla Estéban belong to the state of Sonora.

Phyllodactylus xanti nocticolus Dixon (1964)
New Mexico State Univ. Sci. Bull. 64(1):1–139 (p. 55).

Holotype.—SDSNH 34824 an adult male; Agua Caliente Hot Springs, San Diego Co., California. By Laurence M. Klauber [Charles Shaw and Paul Breese]. Preserved March 8, 1942.

Paratypes.—From San Diego County, as follows: SDSNH 2952, 18633, 32955, 35476–35490, 40073 Yaqui Well; SDSNH 18632, 33247 Sentenac Canyon; SDSNH 18921 Yaqui Pass; SDSNH 33672–33674 Palm Canyon; SDSNH 34825–34827, 43786, 43787 Topotypes; SDSNH 38034, 38041 4 mi W of Vallecitos Stage Station.

Remarks.—=*Phyllodactylus nocticolus nocticolus* according to Murphy (1983, Occ. Papers California Acad. Sci. 137:1–48).

Phyllodactylus xanti sloani Bostic (1972)
Trans. San Diego Soc. Nat. Hist. 16(10):237–263 (p. 252).

Holotype.—SDSNH 45895 an adult female; 23.5 mi SE of El Rosario, Baja California Norte, Mexico. By Dennis L. Bostic, March 31, 1969.

Paratypes.—All from Baja California Norte as follows: SDSNH 45896 1.8 mi NW of Puerto de San Carlos: SDSNH 45897 and 45898 5.4 mi W of Punta Canoas; SDSNH 45899 and 45900 Arroyo San José; SDSNH 45901–45907 Las Palomas; SDSNH 45908 El Cardon; SDSNH 45909–45912 5 mi N of San Javier.

Remarks.—=*Phyllodactylus nocticolus sloani* according to Murphy (1983, Occ. Papers California Acad. Sci. 137:1–48). SDSNH 45912 was "sent to Mexico, 1971" [presumably to Fauna Silvestre, Mexico City].

Sauromalus australis Shaw (1945)
Trans. San Diego Soc. Nat. Hist. 10(15):269–306 (p. 286).

Holotype.—SDSNH 30170 an adult male; San Francisquito Bay, Baja California, Mexico. By Robert S. Hoard, July 30, 1938.

Paratypes.—All are from Baja California Sur as follows: SDSNH 17707 Comondu; SDSNH 17708 La Paz; SDSNH 30168 Loreto; SDSNH 30169 33 mi N of Canipole.

Sauromalus klauberi Shaw (1941)
Trans. San Diego Soc. Nat. Hist. 9(28):285–288 (p. 285).

Holotype.—SDSNH 6859 an adult male; Santa Catalina Island, Gulf of California [Baja California Sur], Mexico. By J. R. Pemberton, December 14, 1931.
Paratypes.—SDSNH 6860 and 6861 data same as for Holotype.
Remarks.—=*Sauromulus ater klauberi* according to Avery and Tanner (1964, BYU Science Bull. 5(3):1).

Sauromalus obesus tumidus Shaw (1945)
Trans. San Diego Soc. Nat. Hist. 10(15):269–306 (p. 292).

Holotype.—SDSNH 27323 an adult male; Telegraph Pass, Gila Mountains, Yuma Co., Arizona. By Laurence M. Klauber, June 15, 1937.
Paratypes.—SDSNH 8613, 27551, 33170–33175, 33224, 33225, 34141, 35090 data same as for Holotype (Gila Mountains, Arizona).

Uma notata cowlesi Heifetz (1941).
Copeia 1941(2):99–111 (p. 104).

Paratypes.—SDSNH 16460–16464 Punta Peñasco, Sonora, Mexico.
Remarks.—=*Uma notata rufopunctata* Cope according to Norris (1958, Bull. Amer. Mus. Nat. Hist. 114(3):251–326). Holotype: CAS 53370 an adult male.

Uta stansburiana klauberi Lowe and Norris (1955)
Hereptologica 11(2):89–96 (p. 91).

Holotype.—SDSNH 6642 an adult male; San Estéban Island, Gulf of California, Sonora, Mexico. By J. R. Pemberton, January 11, 1932.
Paratypes.—SDSNH 3968–3971, 6640, 6641 San Estéban Island, Sonora, Mexico.
Remarks.—=*Uta stansburiana taylori* Smith according to Ballinger and Tinkel (1972, Misc. Pub. Mus. Zool. Univ. Michigan (145):1–83).

Xantusia arizonae Klauber (1931)
Trans. San Diego Soc. Nat. Hist. 7(1):1–16 (p. 3).

Holotype.—SDSNH 5433 an adult female; 1 mi S of Yarnell, Yavapai Co., Arizona. By Philip M. Klauber and Laurence M. Klauber, August 21, 1931.
Paratypes.—SDSNH 5434–5438 data same as for Holotype; SDSNH 5451 and 5452 born (dead) of Holotype in captivity; SDSNH 5450 unborn embryo from SDSNH 5436: SDSNH 5453 unborn embryo from SDSNH 5434.
Remarks.—=*Xantusia vigilis arizonae* according to Bezy (1967 Copeia (3):653–661). SDSNH 5434 was sent to J. R. Slevin at the California Academy of Sciences December 14, 1931.

Serpentes

Arizona elegans blanchardi Klauber (1946)
Trans. San Diego Soc. Nat. Hist. 10(17):311–398 (p. 328).

Paratype.—SDSNH 35343 Schramm, Yuma Co., Colorado.
Remarks.—Holotype: SU 10393 a young adult male; now CAS-SU 10393.

Arizona elegans candida Klauber (1946)
Trans. San Diego Soc. Nat. Hist. 10(17):311–398 (p. 364).

Holotype.—SDSNH 34191 an adult male; Kramer Hills, 6 mi S of Kramer Junction on US 395, San Bernardino Co., California. By James Deuel, June 16, 1941.
Paratypes.—All are from near the type locality in San Bernardino Co., California, as follows: Adelanto: SDSNH 27251, 34187, 34190 16 mi N of; SDSNH 28848, 33980 8 mi N of; SDSNH 31917 12 mi S of; SDSNH 31941, 31942, 35109 3 mi N of; SDSNH 33323 6 mi SW of; SDSNH 33812 6 mi N of; SDSNH 33981, 35093 4 mi S of; SDSNH 33982 14 mi N of; SDSNH 34107 13 mi N of; SDSNH 34150, 35594 2 mi N of. Kramer Hills: SDSNH 28846, 31700, 33795, 35149. Kramer Junction: SDSNH 31766

5 mi N of; SDSNH 31940, 33832, 33983, 34019 8 mi S of; SDSNH 31959 20 mi S of; SDSNH 33826, 34189 3 mi S of; SDSNH 33888, 34164, 34192 5 mi S of; SDSNH 33975, 34017, 35536 7 mi S of; SDSNH 33977, 33978 10 mi S of; SDSNH 33979 12 mi S of; SDSNH 34165 6 mi of; SDSNH 34184 1 mi W of; SDSNH 34185 1 mi E of; SDSNH 34186 11 mi S of; SDSNH 35151, 35537 9 mi S of SDSNH 35654 6.5 mi S of.

Arizona elegans eburnata Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 10(17):311–393 (p. 350).

Holotype.—SDSNH 33094 a young male; Benson's Dry Lake, San Diego Co., California. By James Deuel, June 5, 1940 [preserved].

Paratypes.—All are from near the type locality in San Diego Co., California, as follows: SDSNH 4454, 23854, 23914, 23915, 25437, 25438, 26914, 26939–26942, 27308, 27383, 27405, 29300, 33094, 33095, 17026 Topotypes; SDSNH 4862 Beatty Ranch, Borrego Valley; SDSNH 5136, 21108, 21121 Borrego Valley; SDSNH 23024, 23774–23776, 23852, 23853, 26814, 29301, 29487, 32035 The Narrows; SDSNH 23773 5 mi E of The Narrows; SDSNH 26732 2 mi S of Borrego Post Office; SDSNH 27331 3 mi W of Benson's Dry Lake.

Remarks.—SDSNH 4454, 17026, 21108 were exchanged with H. M. Smith, January 14, 1957 and are presumed to be at the University of Illinois Museum of Natural History. Klauber also gave as paratypes SDSNH 26056 and 26057, but these are actually specimens of *Pituophis melanoleucus deserticola* and *Crotalus viridis oreganus,* respectively; the source of this error is unknown.

Arizona elegans noctivaga Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 10(17):311–398 (p. 343).

Holotype.—SDSNH 34188 a young adult male; 8 mi N of Owlshead, Pinal Co., Arizona. By Charles E. Shaw and Laurence M. Klauber, May 31, 1941.

Paratypes.—All are from Arizona, as follows: Gila Co.: SDSNH 34438 7 mi SE of Globe. Maricopa Co.: SDSNH 15835, 23925, 23926 Sentinel; SDSNH 25829, 26010 Mesa; SDSNH 26913 5 mi S of Wickenburg; SDSNH 26943 Cactus Gardens; SDSNH 32781 Gila Bend; SDSNH 34331 Stanwix. Pima Co.: SDSNH 13724, 29222 Tucson; SDSNH 17949 11 mi N of Tucson; SDSNH 17950, 17951 4½ mi N of Tucson; SDSNH 17952 2 mi N of Tucson; SDSNH 27177 13 mi N of Tucson; SDSNH 27178 4 mi N of Sahuarita; SDSNH 32293 Martinez Hill; SDSNH 32521 11 mi S of Tucson; SDSNH 32714 2 mi NE of Tanque Verde Ranch; SDSNH 34018 14 mi N of Tucson. Pinal Co.: SDSNH 21492, 21493 Picacho; SDSNH 27180 Florence; SDSNH 32323 8 mi W of Casa Grande; SDSNH 34104 3 mi W of Superior; SDSNH 34332 Oracle Junction. Yavapai Co.: SDSNH 17623 1 mi S of Congress Junction. Yuma Co.: SDSNH 34526 5 mi E of Salome.

Arizona elegans pacata Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 10(17):311–398 (p. 379).

Holotype.—SDSNH 17652 an adult male; Santo Domingo (lat. 25°30'N), Baja California Sur, Mexico. By Frank F. Gander, November 16, 1941.

Arizona elegans philipi Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 10(17):311–398 (p. 333).

Holotype.—SDSNH 34456 an adolescent male; 10 mi E of Winslow, Navajo Co., Arizona. By Charles E. Shaw and Carl Engler, July 29, 1941.

Paratypes.—SDSNH 20990 Two Guns, Coconino Co., Arizona; SDSNH 34426 data same as for Holotype.

Charina bottae umbratica Klauber (1943)

Trans. San Diego Soc. Nat. Hist. 10(7):83–90 (p. 83).

Holotype.—SDSNH 12101 an immature male; Fern Valley, near Idyllwild, Riverside Co., California. By Clyde Searl, July 1, 1929.

Remarks.—The validity of *C. b. umbratica* as a subspecies has been questioned on several occasions, whereas in other instances full species status has been proposed. The taxonomic history is treated by Stewart (1977, SSAR Cat. Amer. Amph. Rept. 205.2).

Chilomeniscus stramineus esterensis Hoard (1939)
Pomona College Jour. Ent. and Zool. 31(4):45–46 (p. 45).

Holotype.—SDSNH 30368 an adult male; Estero[s] Salina, Lower [Baja] California, Mexico [24°36'N, 111°49'W]. By R. S. Hoard, July 10, 1938.

Paratypes.—SDSNH 30364–30367, 30369, 30370 data same as for Holotype.

Chionactis occipitalis talpina Klauber (1951)
Trans. San Diego Soc. Nat. Hist. 11(9):141–204 (p. 172).

Paratypes.—SDSNH 39520, 39521 10 mi N of Goldfield, Esmerelda Co., Nevada.

Remarks.—Holotype: CAS 81364 an adult male.

Chionactis palarostris organica Klauber (1951)
Trans. San Diego Soc. Nat. Hist. 11(9):141–204 (p. 178).

Holotype.—SDSNH 40673 an adult male; on the Sonoyta-Ajo road, 9 mi N of the U.S.-Mexican border, in Organ Pipe Cactus National Monument, Pima Co., Arizona. By William R. Supernaugh and Grover E. Steele, May 22, 1950.

Crotalus cerastes cercobombus Savage and Cliff (1953)
Nat. Hist. Misc. 119:1–7 (p. 2).

Paratypes.—All from Arizona, as follows: Maricopa Co.: SDSNH 979–981 18 mi W of Phoenix; SDSNH 17072 10 mi E of Gila Bend; SDSNH 22410–22412 Desert Wells; SDSNH 23879, 23888–23890, 25553–25555, 25854–25857 near Mesa; SDSNH 26915 1 mi S of Morristown; SDSNH 39082 26 mi N of Ajo; SDSNH 39088 1 mi W of Tartron [sic] (see *Remarks*); SDSNH 40893 vicinity of Phoenix. Pima Co.: SDSNH 2324, 2325 Sells; SDSNH 38660 Sonoita (see *Remarks*). Pinal Co.: SDSNH 17068–17071, 17073 3 mi SE of Picacho; SDSNH 25499 5 mi W of Casa Grande; SDSNH 41110–41116, 41362, 41363 4 mi E of Coolidge; SDSNH 41241 4 mi S of Coolidge.

Remarks.—Holotype: SU 7287 an adult male; now CAS-SU 7287. The correct spelling is Tarton. Sonoita is in Santa Cruz Co.

Crotalus cerastes laterorepens Klauber (1944)
Trans. San Diego Soc. Nat. Hist. 10(8):91–126 (p. 94).

Holotype.—SDSNH 34074 an adult male; The Narrows, San Diego Co., California. By Cyrus B. Perkins and Charles Shaw, June 6, 1941.

Paratypes.—All are from within a 13-mile radius of the type locality as follows: SDSNH 1762, 1858, 2209, 2210, 4571, 4572, 4645–4647, 4827, 4875, 4931, 4958, 5052–5055, 5173–5175, 9507, 21098, 21426, 22275, 22357, 23009, 23233, 23640, 23858, 23860, 23917, 23954–23956, 23998, 24006, 24019, 24020, 25423, 25445, 26729–26731, 26823, 26847, 26848, 26857, 26865, 26866, 26937, 26938, 27240, 28113, 28228, 28682, 28683, 28728, 28750, 29085, 29118, 29119, 29271, 29277, 29898, 30719, 31930, 31999, 32307, 32977, 32978, 33044, 33058, 33059, 33123, 33333–33335, 33342, 34035, 34176–34179, 34351, 34570, 35179, 35187, 35188, 35305, 35557–35559, 35597, 35634, 35635.

Crotalus confluentus abyssus Klauber (1930)
Trans. San Diego Soc. Nat. Hist. 6(3):95–144 (p. 114).

Holotype.—SDSNH 2216 an adult male; Tanner Trail, 300 feet below south rim of the Grand Canyon, Coconino Co., Airzona. By E. D. McKee, September 15, 1929.

Paratypes.—None designated.

Remarks.—=*Crotalus viridis abyssus* according to Klauber (1936, Trans. San Diego Soc. Nat. Hist. 8(20):185–276).

Crotalus confluentus kellyi Amaral (1929)
Bull. Antivenin Inst. Amer. 2(4):86–97 (p. 91).

Holotype.—SDSNH 194 a male; Needles [San Bernardino Co.], California. By Mr. O. R. West, July 11, 1926.

Paratype.—SDSNH 195 data same as for Holotype.

Remarks.—=*Crotalus s. scutulatus* according to Klauber (1930, Trans. San Diego Soc. Nat. Hist. 6(3):95–144.

Crotalus confluentus lutosus Klauber (1930)
Trans. San Diego Soc. Nat. Hist. 6(3):95–144 (p. 100).

Holotype.—SDSNH 1814 a young adult male; 10 mi NW of Abraham on the road to Joy, Millard Co., Utah. By Cyrus B. Perkins, May 12, 1929.

Paratypes.—SDSNH 1800–1813, 1815, 1816 20 mi NW of Delta, Millard Co., Utah.

Remarks.—=*Crotalus viridis lutosus* according to Klauber (1936, Trans. San Diego Soc. Nat. Hist. 8(20):195–276).

Crotalus confluentus nuntius Klauber (1935)
Trans. San Diego Soc. Nat. Hist. 8(13):75–90 (p. 78).

Holotype.—SDSNH 3105 an adult male; Canyon Diablo, Coconino Co., Arizona. By R. L. Borden, August 9, 1930.

Remarks.—=*Crotalus viridis nuntius* according to Klauber (1936, Trans. San Diego Soc. Nat. Hist. 8(20):185–276).

Crotalus durissus culminatus Klauber (1952).
Bull. Zool. Soc. San Diego 26:1–143 (p. 67).

Paratype.—SDSNH 43403 Hacienda El Sabino, near Uruapan, Michoacan, Mexico.

Remarks.—Holotype: FMNH 126616 (formerly EHT 5224) a juvenile female. SDSNH 43403 was formerly EHT 5233.

Crotalus mitchelli angelensis Klauber (1963)
Trans. San Diego Soc. Nat. Hist. 13(5):73–80 (p. 75).

Holotype.—SDSNH 51994 an adult male; 4 mi SE of Refugio Bay, Isla Angel de la Guarda, Gulf of California, Mexico. By Dr. Reid Moran, March 22, 1963.

Paratypes.—SDSNH 19717, 19718, 19990–19995, 44358, 51991–51993, 51995, 51996. All are from Isla Angel de la Guarda.

Remarks.—Endemic to Isla Angel de la Guarda.

Crotalus mitchellii [sic] ***muertensis*** Klauber (1949)
Trans. San Diego Soc. Nat. Hist. 11(6):61–116 (p. 97).

Holotype.—SDSNH 37447 an adult male; El Muerto Island, Gulf of California, Mexico. By Charles H. Lowe, Jr., June 6 or 7, 1946.

Paratypes.—SDSNH 37442–37444, 37446, 37448, 37449, 38040 El Muerto Island.

Remarks.—El Muerto Island = Isla Miramar in the San Luis group, Baja California Norte. The correct spelling is *mitchelli*.

Crotalus molossus estebanensis Klauber (1949)
Trans. San Diego Soc. Nat. Hist. 11(6):61–116 (p. 104).

Holotype.—SDSNH 26792 an adult female; San Estéban Island, Gulf of California, Mexico. By an expedition under Capt. G. Allan Hancock, April 17, 1937 (preserved).

Remarks.—Endemic to Isla San Estéban.

Crotalus ruber lorenzoensis Radcliffe and Maslin (1975)
Copeia 1975(3):490–493 (p. 490).

Holotype.—SDSNH 46009 an adult male; San Lorenzo Sur Island, Gulf of California, Baja California Norte, Mexico. By Charles E. Shaw, May 23, 1966.

Paratypes.—SDSNH 6605, 45052, 45053, all from San Lorenzo Island Sur.
Remarks.—Endemic to San Lorenzo.

Crotalus triseriatus anahuacas Gloyd (1940)
Chicago Acad. Sci. Special Publ. No. 4:1–270 (p. 91).

Paratypes.—SDSNH 43404 43 km N of Tres Cumbres, Morelos, Mexico.
Remarks.—Holotype: MCZ 33681 a female. SDSNH 43404 was formerly T-S 5492.

Crotalus triseriatus aquilus Klauber (1952)
Bull. Zool. Soc. San Diego 26:1–143 (p. 24).

Paratypes.—SDSNH 3496–3501, 6575–6577 vicinity of Alvarez, San Luis Potosi, Mexico (Topotypes).
Remarks.—=*Crotallus aquilus* according to Harris and Simmons (1978, Bull. Maryland Herp. Soc. 14(3):105–211). Holotype: MCZ 27843 an adult female.

Crotalus vegrandis Klauber (1941)
Trans. San Diego Soc. Nat. Hist. 9(30):333–335 (p. 334).

Paratypes.—SDSNH 34607 Maturin Savannah, near Uracoa Monagas, Venezuela.
Remarks.—Holotype: CM 17384 an adult male. SDSNH 34607 was formerly CM 17385.

Crotalus viridis caliginis Klauber (1949)
Trans. San Diego Soc. Nat. Hist. 11(6):61–116 (p. 90).

Holotype.—SDSNH 2800 an adult male; South Coronado Island off the northwest coast of Baja California, Mexico. By E. H. Quayle, June 2, 1930.
Paratypes.—SDSNH 2801–2804, 4924–4926, 7538–7540, 11177, 11178, 13711–13715, 20077, 20078 "All probably came from South Coronado Island, Baja California Norte, Mexico."
Remarks.—Known only from the type locality.

Crotalus willardi meridionalis Klauber (1949)
Trans. San Diego Soc. Nat. Hist. 11(8):121–140 (p. 131).

Holotype.—SDSNH 6569 an adult female; Coyotes ["on the railroad to El Sato"], elevation 8000′, Durango, Mexico. By Edmund Heller and Charles M. Barber, August 1904.
Remarks.—SDSNH 6569 was one of two specimens obtained from the Field Museum, both of which were numbered FMNH 1493.

Hypsiglena nuchalatus W. Tanner (1943)
Great Basin Nat. 4(1 & 2):49–54 (p. 49).

Paratypes.—SDSNH 20233, 20293, 22501 Visalia, Tulare Co., California.
Remarks.—=*Hypsiglena torquata nuchulata* according to Bogert and Oliver (1945, Bull. Amer. Mus. Nat. Hist. 83(6):297–426 (p. 381)). Holotype: BYU 3008 a small female.

Hypsiglena ochrorhynchus [sic] ***klauberi*** W. Tanner (1944)
Great Basin Nat. 5(3 & 4):25–92 (p. 71).

Holotype.—SDSNH 20228 a male; South Cornoado [=Coronado] Island, Lower California [Baja California Norte]. By Philip M. Klauber, June 11, 1933.
Remarks.—=*Hypsiglena torquata klauberi* according to Bogert and Oliver (1945, Bull. Amer. Mus. Nat. Hist. 83(6):297–426). A review of the nomenclatural problem surrounding *ochrorhyncha* Cope vs. *torquata* Günther is given by Hardy and McDiarmid (1969:169, Univ. Kansas Publ. Mus. Nat. Hist. 18(3):39–252).

Hypsiglena ochrorhynchus [sic] ***tortugaensis*** W. Tanner (1944)
Great Basin Nat. 5(3–4):25–92 (p. 69).

Paratypes.—SDSNH 4074 Tortuga Island [Baja California Sur, Mexico].

Remarks.—=*Hypsiglena torquata tortugaensis* according to Bogert and Oliver (1945, Bull. Amer. Mus. Nat. Hist. 83(6):297–426). Holotype: CAS 51460 a female (by inference). See also *Remarks* under *H. o. klauberi.*

Hypsiglena torquata catalinae W. Tanner (1966)
Trans. San Diego Soc. Nat. Hist. 14(15):189–196 (p. 192).

Holotype.—SDSNH 44680 an adult male; Santa Catalina Island, approximately 25°38′N, 110°47′W, Gulf of California, Baja California [Sur], Mexico. By George E. Lindsay, June 25, 1964.
Paratypes.—SDSNH 44376, 44681 Topotypes.

Lampropeltus zonata pulchra Zweifel (1952)
Copeia 1952(3):152–168 (p. 162).

Holotype.—SDSNH 38667 an adult male; near Crater Camp [450 ft], Santa Monica Mountains, Los Angeles Co., California.
Remarks.—Date and collector unknown. Apparently received from the San Diego Zoo, preserved August 2, 1947.

Leptotyphlops humilis cahuilae Klauber (1931)
Trans. San Diego Soc. Nat. Hist. 6(23):333–352 (p. 339).

Holotype.—SDSNH 2637 an adult; Yaqui Well by the County Road Camp, San Diego Co., California. By Laurence M. Klauber, May 15, 1930.
Paratypes.—None designated.
Remarks.—Sex of Holotype not given.

Leptotyphlops humilis lindsayi Murphy (1975)
Proc. California Acad. Sci. ser. 4, 40(5):93–107 (p. 96).

Holotype.—SDSNH 44386 an adult female; Marquer Bay, Isla Carmen, Baja California (Sur), Mexico. By Charles E. Shaw and George E. Lindsay, April 4, 1962.
Remarks.—Known only from Holotype.

Lichanura roseofusca gracia Klauber (1931)
Trans. San Diego Soc. Nat. Hist. 6(20):305–318 (p. 307).

Holotype.—SDSNH 2995 a young female; Randsburg, Kern Co., California. By Lucile Rector, June, 1930.
Remarks.—=*Lichanura trivirgata gracia* according to Miller and Stebbins (1964: 189 The Lives of Desert Animals in Joshua Tree Nat'l Monument, Univ. Calif. Press vi + 452 p.) and others since, all without comment. For a discussion see Yingling (1982, SSAR Cat. Amer. Amph. Rept. 294.1).

Masticophis bilineatus lineolatus Hensley (1950)
Trans. Kansas Acad. Sci. 53(2):270–288 (p. 272).

Holotype.—SDSNH 43402 an adult male; 12.9 mi S and 5 mi E of Ajo, Pima Co., Arizona.
Remarks.—SDSNH 43402 was formerly UIMNH 5611.

Masticophis bilineatus slevini Lowe and Norris (1955)
Herpetological 11(2):89–96 (p. 93).

Holotype.—SDSNH 3826 an adult female; San Estéban Island, Gulf of California, Sonora, Mexico. By Mrs. Griffing [Margaret] Bancroft, April 18, 1930.
Paratype.—SDSNH 41571 San Estéban Island, Gulf of California, Sonora, Mexico.

Phyllorhynchus browni lucidus Klauber (1940)
Trans. San Diego Soc. Nat. Hist. 9(20):195–214 (p. 202).

Holotype.—SDSNH 28819 a juvenile female; Enchanto Valley, 7 mi W of Cave Creek, Maricopa Co., Arizona. By V. Housholder, May 21, 1938.

Phyllorhynchus decurtatus nubilus Klauber (1940)
Trans. San Diego Soc. Nat. Hist. 9(20):195–214 (p. 197).

Holotype.—SDSNH 32493 an adult male; Xavier (Weisner's Ranch), Pima Co., Arizona. By Lee Arnold, July 16, 1939.

Paratypes.—From Arizona as follows: Pima Co.: SDSNH 29216 2 mi N of San Xavier Mission; SDSNH 29287 4 mi N of San Xavier Mission; SDSNH 32273 Ajo Junction (Escuela); SDSNH 32289 4 mi S of Ajo Junction; SDSNH 32290 2 mi S of Ajo Junction near Tucson; SDSNH 32468 east base of "A" Mountain; SDSNH 32494 5 mi N of Tucson. Pinal Co.: SDSNH 32274 26 mi N of Tucson.

Remarks.—Klauber noted in his catalogue that SDSNH 29287 and 32468 were "traded to Slevin, 1941"; these are now CAS specimens.

Phyllorhynchus decurtatus perkinsi Klauber (1935)

Bull. Zool. Soc. San Diego 12:1–31 (p. 11).

Holotype.—SDSNH 23757 an adult male; [Benson's] Dry Lake 3 mi W of Imperial Co. Line on Narrows, Kane Springs Road, San Diego Co., California. By Laurence M. Klauber, May 4, 1935.

Paratypes.—SDSNH 22260, 22261, 22295, 22297, 22298, 22741, 22954, 22955, 23027, 23386, 23387, 23750–23756, 23758–23761, 23815, 23846–23848, 23911–23913, 23918–23923, 23951, 23995–23997 all from very near the type-locality.

Pituophis catenifer bimaris Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 11(1):1–40 (p. 7).

Holotype.—SDSNH 32621 an adult male; Santa Gertrudis, near El Arco (lat. 28°N), Baja California, Mexico. By Robert S. Hoard, August, 1939.

Paratypes.—All from Baja California, Mexico, as follows: SDSNH 2934, 2935 El Refugio (northeast of Magdalena Bay); SDSNH 32523 18 mi N of Punta Prieta (lat. 27°N); SDSNH 3813, 11553 San Ignacio; SDSNH 31032 Bahia Thurtoe (1 mi S of Bahia Tortuga); SDSNH 17562 and 17563 Rancho Las Flores (12 mi E of El Arco); SDSNH 1129, 1181 El Mármol.

Remarks.—=*Pituophis melanoleucus bimaris* according to Smith and Kennedy (1951, Hereptologica 7(3):93–96).

Pituophis catenifer coronalis Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 11(1):1–40 (p. 19).

Holotype.—SDSNH 20229 an adult female; South Coronado Island, Baja California Norte, Mexico. By Philip M. Klauber, June 11, 1933.

Paratype.—SDSNH 11365 Coronado Islands, Baja California Norte, Mexico (restricted to South Coronado Island by Klauber, *ibid* p. 20).

Remarks.—=*Pituophis melanoleucus coronalis* according to Smith and Kennedy (1951, Herpetologica 7(3):93–96).

Pituophis catenifer fuliginatus Klauber (1946)

Trans. San Diego Soc. Nat. Hist. 11(1):1–40 (p. 14).

Holotype.—SDSNH 17449 a young adult female; San Martin Island, off the west coast of Baja California, Mexico. By Lewis W. Walker, July 11, 1939.

Paratypes.—SDSNH 17463, 17464 Topotypes.

Remarks.—=*Pituophis melanoleucus fuliginatus* according to Smith and Kennedy (1951, Herpetologica 7(3):93–96).

Pituophis catenifer pumilus Klauber (1946)

Trans. Soc. Diego Soc. Nat. Hist. 11(2):41–48 (p. 41).

Holotype.—SDSNH 17238 a young adult male; Santa Cruz Island, Santa Barbara Co., California. By Norman Bilderback, May 5, 1938.

Remarks.—=*Pituophis melanoleucus pumilis* according to Smith and Kennedy (1951, Herpetologica 7(3):93–96).

Rhinochelus lecontei clarus Klauber (1941)

Trans. San Diego Soc. Nat. Hist. 9(29):289–332 (p. 308).

Holotype.—SDSNH 31440 an adult male; Borrego Valley, 2 mi N of The Narrows, San Diego Co., California. By Richard Neil, May 7, 1939.

Paratypes.—As follows: San Diego County: SDSNH 2631, 11288, 26815, 28650, 31491 Yaqui Well; SDSNH 11349 La Puerta; SDSNH 16998, 26816 San Felipe Valley; SDSNH 17009, 25632, 20849, 20850, 28755, 33022 The Narrows; SDSNH 31445 5 mi W of The Narrows; SDSNH 23442 Benson's Dry Lake; SDSNH 29078, 32993 Borrego Valley; SDSNH 29110, 29514, 33398 Sentenac Canyon (vicinity); SDSNH 33021, 33049, 33060 Scissors Crossing (vicinity). Riverside County: SDSNH 28670 Cathedral City; SDSNH 31503 Indio; SDSNH 32137 Palm Springs R.R. Station.

Remarks.—=*Rhinochelus lecontei lecontei* according to Shannon and Humphrey (1963, Herpetological 19(3):153–160). See also Medica (1975, SSAR Cat. Amer. Amphib. Rept. 175.2).

Salvadora grahamiae virgultea Bogert (1935)

Bull. So. California Acad. Sci. 34(1):88–94 (p. 89).

Holotype.—SDSNH 12025 a young adult male; Deerhorn Flat, San Diego Co., California. By F. E. Walker, June 29, 1929.

Remarks.—=*Salvadora hexalepis virgultea* according to Schmidt (1940, Zool. Ser. Field Mus. Nat. Hist. 24:143–150).

Salvadora hexalepis klauberi Bogert (1945)

Am. Mus. Novit. 1285:1–14 (p. 2).

Holotype.—SDSNH 20912 an adult male; Cape San Lucas, Baja California, Mexico. By Fred Lewis, August 6, 1933 (preserved).

Paratypes.—All from Baja California as follows: SDSNH 3827 San Ignacio; SDSNH 20466, 20511, 20858 Cape San Lucas; SDSNH 30385 3 mi S of Canipole, NW of Loreto; SDSNH 30386 5 mi N of San Xavier Mission; SDSNH 30387 Loreto.

Salvadora hexalepis mojavensis Bogert (1945)

Am. Mus. Novit. 1285:1–14 (p. 6).

Paratypes.—As follows: Arizona: Mojave Co.: SDSNH 17315 Lucky Star Mine, Chemehuevis Mountains; SDSNH 25385 White Hills, 28 mi N of Chloride. Coconino Co.: SDSNH 34439 9 mi W of Cameron. California: Inyo Co.: SDSNH 25384 Towne's Pass, Panamint Mountains; SDSNH 28578 Linnie; SDSNH 32827 Daylight Pass, Funeral Mountains; SDSNH 34100 3 mi SW of Wildrose Station. Kern Co.: SDSNH 25864 2 mi N of Grapevine Station; SDSNH 26130 20 mi S of Inyokern. San Bernardino Co.: SDSNH 4400, 4401, 33446 Mountain Pass, Ivanpah Mountains; SDSNH 8503 Twenty-nine Palms; SDSNH 10692 Klinefelter; SDSNH 33951 Hawes; SDSNH 35896 7 mi W of Red Pass, NE of Barstow. Nevada: Clark Co.: SDSNH 25357 13 mi W of Indian Springs; SDSNH 25386 19 mi SE of Indian Springs near Corn Creek.

Remarks.—Holotype: AMNH 63000 an adult male.

Sonora bancroftae Klauber (1943)

Trans. San Diego Soc. Nat. Hist. 10(4):69–70 (p. 69).

Holotype.—SDSNH 35077 a female; 2 mi E of San Jorge, Lower California, Mexico. By Mrs. Griffing [Margaret] Bancroft, April 10, 1942.

Remarks.—=*Sonora semiannulata* according to Frost (1983, Trans. Kansas Acad. Sci. 86(1):31–37).

Sonora occipitalis klauberi Stickel (1941)

Bull. Chicago Acad. Sci. 6(7):135–140 (p. 138).

Holotype.—SDSNH 29647 an adult male; Tucson, Pima Co., Arizona. By C. T. Vorhies, June 3, 1938.

Paratype.—SDSNH 17115 3 mi SE of Picacho, Pinal Co., Arizona.

Remarks.—=*Chionactus occipitalis klauberi* according to Stickel (1943, Proc. Biol. Soc. Wash. 56:109–128).

Sonora palarostris Klauber (1937)
Trans. San Diego Soc. Nat. Hist. 8(27):363–366 (p. 363).

Holotype.—SDSNH 26771 an adult male; 5 mi S of Magdalena, Sonora, Mexico. By George Lindsay, April, 1937.

Remarks.—=*Chionactis palarostris palarostris* according to Klauber (1951, Trans. San Diego Soc. Nat. Hist. 11(9):141–204).

Tantilla eiseni transmontana Klauber (1943)
Trans. San Diego Soc. Nat. Hist. 10(5):71–74 (p. 71).

Holotype.—SDSNH 29273 an adult male; 1 mi E of Yaqui Well, San Diego Co., California. By Charles Shaw and Cyrus Perkins, June 6, 1938.

Paratypes.—From California as follows: Riverside Co.: SDSNH 33760, Palm Springs. San Diego Co.: SDSNH 2633, 2634 Yaqui Well; SDSNH 11260 La Puerta; SDSNH 32419, 33997 Sentenac Canyon.

Remarks.—=*Tantilla planiceps transmontana* according to Tanner (1966, Herpetologica 22(2):134–152) and *Tantilla planiceps* according to Cole and Hardy (1981: 268, Bull. Amer. Mus. Nat. Hist. 171(3):199–284), who regard the species as monotypic.

Trimorphodon biscutatus semirutus Smith (1943)
Proc. U.S. Natl. Mus. 93(3169):393–504 (p. 492).

Paratype.—SDSNH 43401 10 mi N of Tafetán, Michoacan, Mexico.

Remarks.—=*Trimorphodon biscutatus biscutatus* according to Duellman (1954, Occ. Pap. Mus. Zool. Univ. Michigan 560:1–24). Holotype: USNM 110410 a male (cited as EHT-HMS 23619 in Smith 1943).

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Caudata

Plethodon richmondi Netting and Mittleman (1938)
Ann. Carnegie Mus. 27:287–293 (p. 288).

Paratype.—SDSNH 32680 Oglebay Park near Wheeling, Ohio Co., West Virginia.

Remarks.—Holotype: CM 14189 an adult male. SDSNH 32680 was formerly CM 5296.

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Imocaris tuberculata, n. gen., n. sp. (Crustacea: Decapoda) from the upper Mississippian Imo Formation, Arkansas

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Abstract. A new genus and species of decapod crustacean is described from the Upper Mississippian Imo Formation, near Leslie, Arkansas. The exceptionally well-preserved specimen is a single carapace, associated with a molluscan dominated fauna including ammonoids, gastropods, and bivalves. *Imocaris tuberculata* serves to help fill the stratigraphic gap between the oldest decapod, *Palaeopalaemon newberryi* in the Upper Devonian of Ohio and Iowa, and the diverse Triassic decapod faunas of Europe.

Introduction

Schram et al. (1978) redescribed *Palaeopalaemon newberryi* Whitfield, 1880, and recognized it as the earliest decapod crustacean. However, until now, there has been a significant gap in the decapod fossil record from this Upper Devonian form to the better known Triassic decapods of central Europe (see e.g., Förster, 1967). The specimen described herein is a single well-preserved carapace from the Upper Mississipian-Chesterian (Naurian-Arnsbergian; ammonoid zone E_2b-c) of Arkansas interpreted to be a decapod crustacean.

This specimen was collected from a road cut along Peyton Creek just south of the Van Buren Co. line, Arkansas, along U.S. Hwy. 65 approximately 6.4 km (4 mi) southeast of Leslie, Arkansas. The fossil was found as the result of washing and concentrating some 817 kgs of matrix from a 0.6 m (2 ft) concretionary shale layer approximately 32 m (105 ft) above the contact of the Imo Formation with the underlying Pitkin Formation (in the middle of "bed 21," of Sutherland and Manger 1977, fig. 1).

Systematic paleontology

Order Decapoda Latreille, 1803
Suborder Pleocyemata Burkenroad, 1963
Infraorder Reptantia Boas, 1800
Section Brachyura Latreille, 1803
Subsection Dromiacea de Haan, 1833
Genus *Imocaris* n. gen.

Diagnosis.—Carapace cylindrical, with subrectangular outline in both dorsal and lateral views. Surface tuberculate. Cervical and branchiocardiac grooves prominent. Rostrum small to non-existent. Antero-lateral margin with prominent denticles.

Etymology.—Named after the Imo Formation, gender feminine.

Type species.—*Imocaris tuberculata* n. sp.

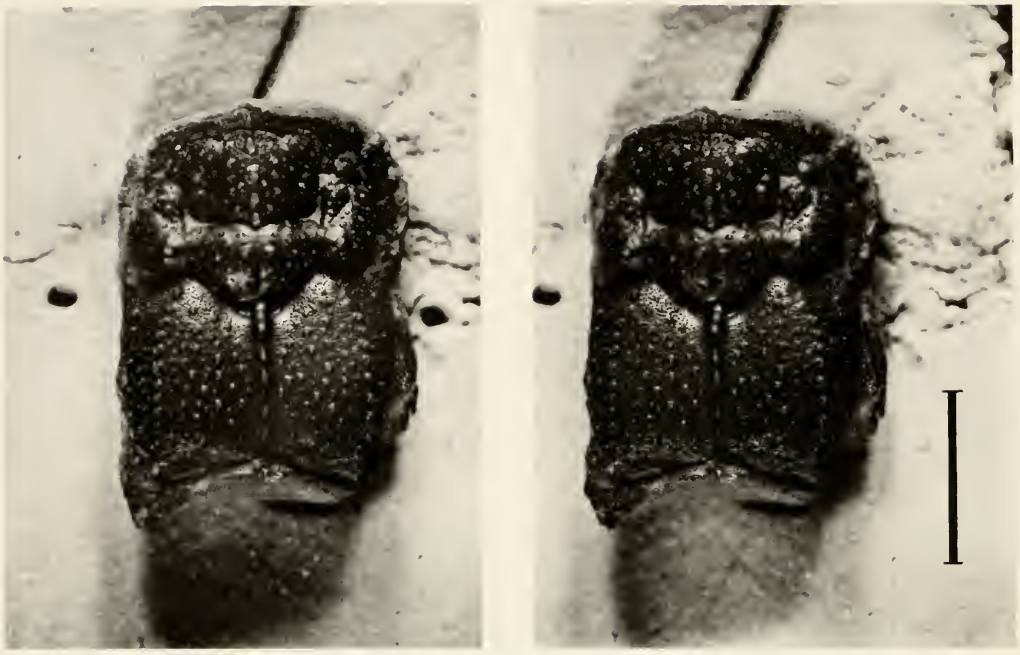

FIGURE 1. *Imocaris tuberculata* n. sp., holotype SDSNH 25139, stereo pair, scale = 5 mm.

Imocaris tuberculata n. sp.
Figure 1

Diagnosis.—Because there is but one species, the diagnosis is the same as that of the genus.

Holotype.—SDSNH 25139 (Fig. 1).

Locality.—SDSNH loc. 3191; NE ¼, sec. 11, T.13N., R.15W.; along road cut in U.S. Hwy. 65, south of Van Buren Co. line, Arkansas, on Peyton Creek.

Stratum.—Imo Formation, Chesterian, Upper Mississippian.

Etymology.—After the tuberculate nature of the carapace.

Description.—Anterior margin of carapace straight, without orbits, with only slight suggestion of rostrum. Lateral margin anterior of branchiocardiac groove with at least 5 prominent denticles, and posterior of branchiocardiac groove marked by submarginal furrow. Posterior margins slightly concave, with faint submarginal furrow. Prominent, deep cervical and branchiocardiac grooves, cervical grooves extend laterally from mid-line and turn anteriad as short antennar grooves, branchiocardiac grooves continuous laterally with prominent inferior grooves. Carapace surface tuberculate. Mid-dorsal line marked by row of 4 large tubercles between rostral area and cervical groove, by slight groove between the cervical and branchiocardiac grooves, and by clear ridge surmounted by row of 5 (?6) tubercles between branchiocardiac groove and posterior margin. Pair of tubercle rows located laterally between branchiocardiac groove and posterior margin about ½-way between median ridge and lateral margins, forming planes at which curvature of posterior carapace surface changes from horizontal to more vertical orientation. Carapace mid-line length—11 mm, approximate lateral margin length—12 mm, width—9.5 mm.

Remarks.—The fossil preserves an excellent view of the dorsal surface of the carapace. Attempts at preparation of the underside and margins of the specimen, however, seem to indicate that only the carapace is fossilized, i.e., no ventral thoracic structures appear to be present.

Discussion

The higher taxonomic affinity of any Paleozoic decapod is of interest because of the understanding it might lend to elucidating the sequence of events in the early radiation of Decapoda. Paleozoic decapods have been rare and widely scattered geographically. The type specimens of the supposed Permian decapod carapaces from Sicily, *Palaeopemphix* Gemmellaro, 1890, have been lost and, thus, their suggested decapod versus cumacean affinities can never be verified. The Devonian *Palaeopalaemon newberryi,* preserved in great detail, possesses several features in a combination of both astacidean and palinuran reptants (Schram et al. 1978); and, in addition, Felgenhauer and Abele (1983) have noted a characteristic natatian feature in that form as well, viz., the large scaphocerite. Bachmeyer and Malzahn (1983) have recorded from the Upper Permian Zechstein of Germany a free decapod cheliped (given the name *Erymastacus ? hoerstgenensis*), as well as leg and carapace fragments attributed to decapods in the stomach contents of the chimaeriform fish *Janassa bituminosa.* The fragmentary nature of the Zechstein fossils, however, makes them difficult to compare to the other known Paleozoic decapod whole body fossils. Finally, little can be said about the Soviet Permian form *Protoclytiopsis antiqua* Birshtein, 1958, except that it appears to be taxonomically close to a large, reptant, glypheoid type (Schram 1980).

Several characters mark *Imocaris tuberculata* as unusual, viz., the cylindrical form and rectangular proportions of the carapace, the presence of only a branchiocardiac groove posterior to the cervical (or alternatively a fusion of the post-cervical and branchiocardiac grooves), the lack of orbits, and the small or absent rostrum. Unfortunately, the lack of preservation of any eyes, antennae, mouthparts, thoracopods, and abdomen makes a definitive higher taxonomic assignment difficult.

Quite unexpectedly, the closest analogs to the derived features of *Imocaris tuberculata* listed above are to be found among the dromiacean brachyurans. These living forms tend to possess markedly cylindrical and somewhat subrectangular carapaces, strong cervical and branchiocardiac grooves, absent or poorly developed orbits, frequently weakly developed rostra, and (in at least the prosopids, some dynomenids, and the homoloids) prominent carapace sculpturing. The assignment of *Imocaris* to the dromiaceans on the basis of this single specimen considerably extends the range of that taxon back from the Lower Jurassic into the middle of the Carboniferous.

The recognition of *Imocaris* as a decapod begins to fulfill the expectations of Schram et al. (1978) that an extensive Paleozoic radiation of Decapoda is to be discovered in upper Paleozoic strata.

Acknowledgments

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Literature Cited

Bachmeyer, F., and E. Malzahn. 1983. Der erste Nachweis eines decapoden Krebses im niederrheinischen Kupferschiefer. Annalen des Naturhistorischen Museums in Wien. 85/A:99–106.

Birshtein, Ya. A. 1958. Drevneishii predsta vitel otryada desyatinogikh rakoobraznikh, *Protoclytiopsis antiqua,* in Permakikh otlozhenii zapadnoi Sibiri. Doklady Akademii Nauk SSSR 122:477–480.

Felgenhauer, B. E., and L. G. Abele. 1983. Phylogenetic relationships among shrimp-like decapods. Crustacean Issues 1:291–311.

Förster, R. 1967. Die reptanten Dekapoden der Trias. Neues Jahrbuch fur Geologie und Paleontologie Abhandhungen 128:136–194.

Gemmellaro, G. G. 1890. Crostacei dei calcari con Fusulina della Valle del Fiume Sosio, nella provicia di Palermo in Sicilia. Società Italiana di Scienze Naturali, Memorie (3)8:1–40.

Schram, F. R. 1980. Notes on miscellaneous crustaceans from the Late Paleozoic of the Soviet Union. Journal of Paleontology 54:542–547.

———, R. M. Feldmann, and M. J. Copeland. 1978. The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. Journal of Paleontology 52:1375–1387.

Sutherland, P. K., and W. L. Manger. 1977. Upper Chesterian-Morrowan Stratigraphy and the

Mississippian-Pennsylvanian Boundary in Northeastern Oklahoma and Northwestern Arkansas. Oklahoma Geological Survey Guidebook 18. University of Oklahoma, Norman.

Whitfield, R. P. 1880. Notice of new forms of fossil crustaceans from the Upper Devonian rocks of Ohio, with description of new genera and species. American Journal of Science (3)19: 33–42.

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New material of *Hydrodamalis cuestae* (Mammalia: Dugongidae) from the Miocene and Pliocene of San Diego County, California

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Abstract. The geology, faunal content, and age of sirenian-bearing marine rocks in San Diego County, southern California, are reviewed and reevaluated. The San Mateo Formation comprises two members, respectively of Late Miocene (late Clarendonian or, more likely, early Hemphillian) and Early Pliocene (late Hemphillian) age. The San Diego Formation also includes two members, both probably of Late Pliocene (Blancan) age, though the upper member may extend into the Early Pleistocene. All four members have yielded new specimens of sirenians, most or all of which represent *Hydrodamalis cuestae* Domning 1978. These specimens extend our knowledge of the osteology of this species, and confirm the supposition that the holotype is abnormal in several respects. During the Hemphillian, the juveniles of the species had an upper dentition probably consisting of DP^{2-5}; it is still unknown whether later Pliocene juveniles retained teeth. A braincase from the San Diego Formation is the largest known of any sirenian, probably representing an individual over 10 m long and confirming the previous observation that *Hydrodamalis* grew larger in California than at Bering Island.

Introduction

Domning (1978) reviewed the fossil record of North Pacific sirenians and described the new species *Hydrodamalis cuestae,* a form intermediate between the Late Miocene *Dusisiren jordani* (Kellogg 1925) and the Late Pleistocene-Recent *H. gigas* (Zimmermann 1780) (Steller's sea cow). The holotype of *H. cuestae* came from the Upper Pliocene (Blancan) Pismo Formation in San Luis Obispo County, California, and referred specimens came from the Hemphillian San Mateo Formation in San Diego County, the Hemphillian Capistrano Formation in Orange County, and an unnamed Pliocene unit in Baja California, Mexico. A single thoracic vertebra from the Blancan San Diego Formation near Tijuana, Mexico, was identified only as *Hydrodamalis* species.

Since 1978, a number of additional specimens of *Hydrodamalis cuestae* have been obtained by the San Diego Natural History Museum from the San Mateo and San Diego Formations in San Diego County. These clarify some of the problems posed by the previously known material; in particular, they show that certain anomalous features of the holotype, thought by Domning (1978) to be pathological, are indeed atypical of the species.

Abbreviations used are as follows: SDSNH, San Diego Society of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; USNM, U.S. National Museum of Natural History, Washington, D.C.

Geology and Age of the Deposits

Remains of fossil hydrodamalines from San Diego County, California, have been recovered from both the Upper Miocene-Lower Pliocene San Mateo Formation (Hemphillian) at Oceanside and the Upper Pliocene San Diego Formation (Blancan) at San Diego. These rock units accumulated in separate sedimentary basins and contain distinctly different marine vertebrate assemblages.

San Mateo Formation

Barnes (1976) and Barnes et al. (1981) have tentatively assigned the vertebrate-producing marine beds at Oceanside to the San Mateo Formation of Woodford (1925). This rather poorly defined rock unit has been mapped from the type area near San Clemente throughout the coastal portion of Camp Pendleton Marine Corps Base as far south as the city of Oceanside (Moyle 1973, Young and Berry 1981). The best exposures of the San Mateo Formation at Oceanside are in the Lawrence Canyon area adjacent to the San Luis Rey River (Fig. 1). Here erosion, grading, and quarry operations have combined to produce a number of natural and artificial outcrops.

Lawrence Canyon is aligned in part along a north-south striking, eastward-dipping, high angle normal fault. The San Mateo Formation is confined to the east side of this fault where it rests unconformably on westward-dipping strata of the Middle Miocene San Onofre Breccia and in turn is overlain unconformably by flat-lying Upper Pleistocene, nonmarine terrace deposits. In Lawrence Canyon the San Mateo Formation is approximately 24 m thick and, as noted by Barnes et al. (1981), is divisible into a lower and an upper unit. The lower unit consists of white, fine-grained, massive, friable, micaceous sandstones with occasional green or black claystone lenses and locally common pebbles and cobbles. The upper unit is a complexly bedded sequence of gravels, pebble to cobble conglomerates and friable sandstones. A sharp unconformity marked in places by scour and fill features separates the upper gravel conglomerate unit from the lower white sandstones. Marine vertebrate fossils have been collected from both the upper and the lower unit (Barnes 1976, Domning 1978, Barnes et al. 1981, Howard 1982) whereas invertebrate fossils are conspicuously absent. Barnes et al. (1981) have assigned the vertebrate fossil assemblages from the lower and upper units to the San Luis Rey River Local Fauna and the Lawrence Canyon Local Fauna, respectively.

Fossils in the lower white sandstones generally occur as single isolated elements and occasionally as associated partial skeletons. In contrast, fossils from the upper gravel conglomerate unit are often concentrated in distinct "bone horizons." One particular horizon (SDSNH locality 3161) is a 1.2 m thick, fining-upward sequence divisible into four lithologic units: 1) a basal clast-supported pebble to cobble conglomerate; 2) a matrix-supported pebble conglomerate; 3) an interval of poorly bedded sandstones and gravels with laminated fine-grained sandstone lenses; and 4) thickly laminated fine- and coarse-grained sandstones. Fossils are concentrated in the matrix-supported pebble conglomerate and generally occur as broken and abraded fragments of large bones or as complete and differentially preserved smaller resistant elements. Particularly common are shark teeth, cetacean earbones, and bird humeri and ulnae. Larger bones generally occur in association with the larger pebbles or cobbles, suggesting size-sorting by currents. Apparently the fossils were transported and deposited as biogenic clasts within the traction load.

In terms of general depositional environments it appears that the lower white sandstone unit was deposited under "normal" marine conditions, perhaps at middle to inner shelf depths. The dominance of sandstones over finer-grained lithologies would support this idea of shallow water deposition, although without a preserved benthonic assemblage (e.g., mollusks) it is not possible to make any definite paleobathymetry estimates. Clearly, however, because of the rich marine vertebrate assemblage, this is a marine unit.

The upper gravel conglomerate unit, in contrast to the lower white sandstones, is characterized by complex bedding and very coarse-grained lithologies. The bedding

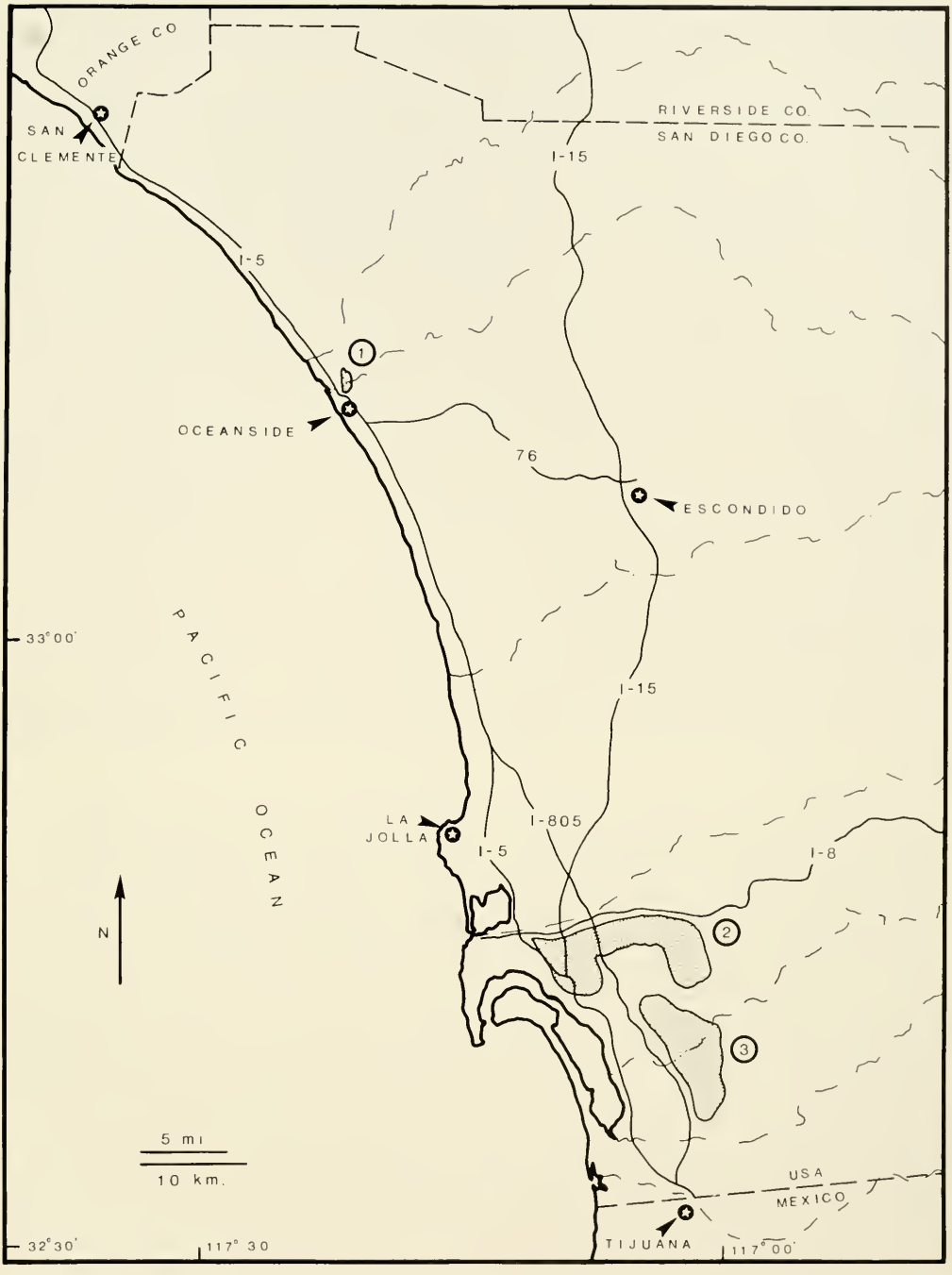

FIGURE 1. Index map of western San Diego County showing the principal outcrop areas of rocks containing *Hydrodamalis cuestae*. 1, Hemphillian San Mateo Formation, Lawrence Canyon; 2, Blancan San Diego Formation, northern San Diego Mesa; 3, Blancan San Diego Formation, Chula Vista/National City area.

features are interpreted as representing anastomosing channel-fill deposits and, together with the coarse-grained lithologies, suggest a fluvial environment. However, the occurrence of common marine vertebrate fossils (not reworked from the lower unit) points instead to a marine environment. The model herein proposed to accommodate these

apparently conflicting environmental settings involves deposition of the upper gravel conglomerate unit at the distal, submarine margin of a river-dominated gravel-cobble delta.

Fossil remains of *Hydrodamalis cuestae* occur in both the San Luis Rey River Local Fauna (lower white sandstone unit) and the Lawrence Canyon Local Fauna (upper gravel conglomerate unit). Both local faunas contain a variety of taxa including sharks, rays, bony fishes, sea birds, fur seals, walrus, and toothed and baleen whales (Barnes et al. 1981). Recent work by personnel at the San Diego Natural History Museum has added additional taxa, especially species of birds (R. M. Chandler, *personal communication*), to the published faunal lists of Barnes et al. (1981) and Howard (1982). To the San Luis Rey River Loca Fauna can be added the white shark *Carcharodon megalodon* Agassiz, a new large species of the flightless auk *Praemancalla,* a shearwater (*Puffinus* species), an eagle (Accipitriformes), a mysticete (Balaenopteridae), and the camel *Aepycamelus* species (S. D. Webb, *personal communication*). To the Lawrence Canyon Local Fauna can be added a billfish (Istiophoridae), a cormorant (*Phalacrocorax* species), a shearwater (*Puffinus* species), the loon *Gavia concinna* Wetmore, an albatross (*Diomedea* species), a mysticete (Balaenopteridae), a llama (cf. *Hemiauchenia* species; S. D. Webb, *personal communication*), and a peccary (Tayassuidae). These last two taxa and the camel (*Aepycamelus* species) are part of a small terrestrial mammal assemblage from the San Mateo Formation which also includes horses of the genus *Dinohippus* (or possibly *Pliohippus*; B. J. MacFadden, *personal communication*).

Barnes et al. (1981) have used the joint occurrence of the horse (*Pliohippus* or *Dinohippus*) and the sabertoothed salmon *Smilodonichthyes rastrosus* Cavender and Miller to correlate both the upper and lower unit of the San Mateo Formation at Oceanside with the Hemphillian North American Land Mammal Age. The recent recovery of an isolated M^2 belonging to the camelid *Aepycamelus* species from the lower white sandstone unit offers a refinement of this correlation and suggests that the San Luis Rey River Local Fauna is of late Clarendonian or early Hemphillian age (Webb et al. 1981).

As suggested by Howard (1982), the avifauna of the San Mateo Formation (especially the mancalline taxa) may offer a means for finer biostratigraphic resolution in the section. The occurrence of the genus *Praemancalla* in the lower unit and the genus *Mancalla* in the upper unit is the basis for this biostratigraphy. Previously, the genus *Praemancalla* was known only from Clarendonian-aged rocks (Monterey Formation) in Orange County (Howard 1976), with two species assigned to this genus. The older species *P. lagunensis* Howard is recorded from the lower part of the Monterey Formation in Orange County, while *P. wetmorei* Howard is recorded from the upper part of the formation. Howard (1982) referred material from the lower white sandstone unit at Oceanside to *P.* species cf. *P. wetmorei,* noting that this was the first Hemphillian record of *Praemancalla.* In the upper gravel conglomerate unit *Praemancalla* is replaced by the genus *Mancalla,* represented here by three species, *M. cedrosensis* Howard, *M. milleri* Howard, and *M. diegensis* (Miller). The co-occurrence of these three species appears to define a useful assemblage zone. Howard (1982:13) has suggested that a considerable hiatus is represented by the unconformity within the San Mateo Formation, one that allowed ". . . time for the demise of the *Praemancalla* and the evolution of *Mancalla.*" It seems then, that the range of *Praemancalla* defines a biostratigraphic interval and that the hiatus in the San Mateo Formation may be represented elsewhere by an additional and younger biozone. From discussions with R. M. Chandler (*personal communication*) it seems that such a biozone is preserved in mudstones of the Capistrano Formation at San Clemente. Here an avifauna was recovered which contains *Mancalla californiensis* Lucas, *M. cedrosensis,* and the auklet *Cerorhinca minor* Howard. (Unfortunately it has not been possible to place the stratigraphic position of this fossil locality within a composite section for the very thick and long-ranging Capistrano Formation.) Apparently this assemblage zone is also preserved within the basal portion of the Almejas Formation on Cedros Island, Baja California, Mexico, where Howard (1971) recorded *M. cedrosensis* and *C. minor* (although without *M. californiensis*).

To summarize these assemblage zones, we then have: *Praemancalla lagunensis* in the Monterey Formation (Clarendonian); *P. wetmorei* in the Monterey Formation (Clarendonian) and "lower" San Mateo Formation (late Clarendonian or early Hemphillian); *Mancalla cedrosensis* and *Cerorhinca minor* with or without *M. californiensis* in the Upper Miocene portions of the Almejas Formation (Hemphillian) and Capistrano Formation (Hemphillian); *M. cedrosensis, M. milleri,* and *M. diegensis* in the "upper" San Mateo Formation (late Hemphillian); and to complete the zonation, *M. milleri, M. diegensis,* and *M. emlongi* Olson in the San Diego Formation (Blancan). (These correlations and age assignments are based in part on the work of Barnes 1976, Repenning and Tedford 1977, Howard 1978, 1982, and R. M. Chandler, *personal communication.*) Whether the "lower" San Mateo Formation is late Clarendonian or early Hemphillian in age cannot at this time be resolved biostratigraphically. However, physical stratigraphy tends to support an early Hemphillian age assignment. Vedder (1972) has suggested that the San Mateo Formation (at least in the type area) may be a channel facies within the lower part of the Capistrano Formation. Similarly, Ehlig (1979) has mapped the San Mateo Formation near San Onofre as a member of the Capistrano Formation. Although the nomenclatural standing of the San Mateo Formation is questionable (it is retained here pending completion of ongoing field work at Camp Pendleton), its correlation with the Hemphillian Capistrano Formation (and not the Clarendonian-aged Monterey Formation) appears to be certain. Thus the lower white sandstones at Oceanside probably are correlative with the basal portion of the Capistrano Formation (Upper Miocene, early Hemphillian), while the upper gravel conglomerate unit at Oceanside probably correlates with some horizon near the top of the Capistrano Formation (Lower Pliocene, late Hemphillian). Howard (1982) has proposed a similar Late Miocene-Early Pliocene correlation for the San Mateo Formation at Oceanside, in contrast to the strictly Miocene age assignment of Barnes et al. (1981).

San Diego Formation

The geology of the marine Pliocene San Diego Formation has recently been summarized by Deméré (1983). This rock unit extends in a broad area of outcrop throughout much of the southwestern portion of San Diego County (Fig. 1). The formation is fossiliferous throughout this area of outcrop and contains a diverse and well-preserved assemblage of both marine invertebrate and vertebrate taxa.

The San Diego Formation was deposited during a marine transgression of the Neogene San Diego Basin, which like other onshore sedimentary basins in southern California (e.g., Ventura Basin, Los Angeles Basin) is structurally related to the wrench and extensional tectonics of the continental borderland. Deposition began during the Late Pliocene and possibly continued into Early Pleistocene time, accumulating at least 75 m of marine and 9 m of nonmarine sedimentary rocks. The overall stratigraphic sequence suggests a successive filling and shallowing of this basin. It is now apparent that extensional tectonics have controlled both the initial deposition as well as the present outcrop distribution of this rock unit. Numerous high-angle normal faults striking north to northwest cut the area into a series of fault blocks which expose different portions of the Pliocene section.

In an attempt to correlate these various fault blocks, Deméré (1983) has informally subdivided the San Diego Formation into a "lower" and an "upper" member using both lithologic and paleontologic criteria. The "lower" member is characterized by yellowish, very fine-grained, massive, friable, micaceous sandstones with locally well-bedded sequences of laminated and cross-bedded sandstones, pebble to cobble conglomerates and well-cemented shell beds. This "lower" member is richly fossiliferous and has produced the bulk of the marine invertebrate fauna so well known through the work of Grant and Gale (1931) and Hertlein and Grant (1944, 1960, 1972). In addition, the diverse avifaunas (Howard 1949, Miller 1956) and cetacean assemblages

(Barnes 1973, 1976) reported from the San Diego Formation have been largely collected from the "lower" member.

Lithologically the "upper" member is characterized by well-bedded sequences of pebble to cobble conglomerate, well-cemented fossiliferous sandstones, and medium- to coarse-grained friable sandstones. Marine invertebrate fossils are locally common in this member, which to date has produced only a few vertebrate remains.

Vertebrate fossils in the San Diego Formation generally occur as single isolated skeletal elements, although occasionally partial or complete skeletons are found. A few rare "bone beds" containing concentrated, unassociated elements have recently been discovered in the formation. To date, the most productive fossil sites have been in the Mission Hills area near downtown San Diego and in the eastern portions of National City and Chula Vista. In these areas large-scale grading operations have provided very extensive exposures of the San Diego Formation, although in most cases these new exposures are accessible for only a short period of time because of development and construction.

Found in association with the vertebrates are rich assemblages of marine macroinvertebrates, primarily mollusks, which provide both biostratigraphic and paleoenvironmental control. The "lower" member contains a middle to outer shelf molluscan fauna characterized by *Patinopecten healeyi* (Arnold), *Pecten stearnsii* Dall, *Lucinoma annulata* (Reeve), and *Opalia varicostata* (Stearns). In contrast, mollusks from the "upper" member indicate deposition in littoral to inner shelf depths. Characteristic species include *Pecten bellus* (Conrad), *Argopecten hakei* (Hertlein), and *Nucella lamellosa* Gmelin along with the echinoid *Dendraster ashleyi* (Arnold). Both members reflect normal marine deposition in a broad coastal embayment probably similar to present-day Monterey Bay along the central California coast.

Fossil remains of *Hydrodamalis cuestae* have been recovered from both the "lower" and "upper" members of the San Diego Formation. As presently understood, the aggregate vertebrate faunule from the "lower" member consists of 7 species of sharks and rays, more than 50 species of bony fishes (most of which are known only from otoliths), 24 species of sea birds, an otariid and a dusignathine (odobenid) pinniped, 7 odontocetes, 10 mysticetes, and the sirenian. A few terrestrial mammal taxa including horse (*Equus* species), camel (cf. *Titanotylopus* species), peccary (cf. *Platygonus* species; M. O. Woodburne, *personal communication*), and gomphothere (*Stegomastodon* cf. *S. rexroadensis* Woodburne) occur in association with the diverse marine vertebrate assemblage. The "upper" member has produced only three vertebrate taxa to date: an albatross (*Diomedea* species), a mysticete (cf. Balaenopteridae), and the sirenian.

Barnes (1976) has correlated the San Diego Formation ("lower" member) with the Blancan North American Land Mammal Age. This correlation, based on the occurrence of the horse *Equus,* is supported by the recent discovery of teeth referable to the gomphothere *Stegomastodon* cf. *S. rexroadensis* (M. O. Woodburne, *personal communication*). Relying on the stratigraphic ranges of molluscan species, the "lower" member is correlative with the San Joaquin Formation in the San Joaquin Basin, the Careaga Formation in the Santa Maria Basin, and the Niguel Formation and the upper Fernando Formation in the southeastern Los Angeles Basin, all Late Pliocene in age (Woodring and Bramlette 1950, Vedder 1972). In turn, the "upper" member of the San Diego Formation correlates with the lower part of the Santa Barbara Formation in the Ventura Basin, which is considered to be Late Pliocene to Early Pleistocene in age (Keen and Bentson 1944). The meager microfossil evidence available (Ingle 1967, Mandel 1973) suggests that the San Diego Formation is apparently no older than planktonic foraminiferal zone N.21 (approximately 3.0 million years B.P., Late Pliocene) and is *perhaps* as young as the *Emiliania annula* calcareous nannoplankton subzone (approximately 1.5 million years B.P., Early Pleistocene; E. D. Milow, *personal communication*). This Pleistocene correlation is tenuous at the moment and must await completion of additional field work for confirmation. It should not be interpreted to mean that the entire "upper" San Diego Formation is Pleistocene.

Systematics

Order Sirenia
Family Dugongidae
Subfamily Hydrodamalinae
Hydrodamalis cuestae Domning, 1978

Material

San Mateo Formation

San Luis Rey River Local Fauna (of Barnes et al. 1981).—

SDSNH locality 2957 (=UCMP loc. V68144), Loretta St., Oceanside:

SDSNH 22655: Two rib fragments. Coll. J. W. Tobiska, I 1979.

SDSNH locality 3004 (=UCMP loc. V68145), Loretta St., Oceanside:

SDSNH 21076: Juvenile left maxilla. Coll. T. A. Deméré, 15 III 1980.

SDSNH locality 3134 (=UCMP loc. V68147), Lawrence Canyon, Oceanside:

SDSNH 23384: Proximal end of rib. Coll. R. A. Cerutti, 22 III 1981.

Lawrence Canyon Local Fauna (of Barnes et al. 1981).—

SDSNH locality 3161 (=UCMP loc. V68106), Lawrence Canyon, Oceanside:

SDSNH 24413: Fragment of juvenile left maxilla. Coll. SDSNH party, VII 1982.
SDSNH 24454: Rib fragment. Coll. SDSNH party, VII 1982.
SDSNH 24685: Immature right humerus. Coll. B. O. Riney and R. A. Cerutti, 26 VI 1982.
SDSNH 24686: Proximal end of juvenile ?right ulna. Coll. SDSNH party, VII 1982.

San Diego Formation

"Lower" Member.—

SDSNH locality 2970-B, Washington St., San Diego:

SDSNH 21685: Rib fragment. Coll. R. A. Cerutti, IX 1980.

SDSNH locality 3148, California St., San Diego:

SDSNH 23719: Vertebrae C1–2, C6–7, T1–?6. Coll. R. A. Cerutti and T. A. Deméré, 16 II 1981.

SDSNH locality 3172, Florida Canyon, San Diego:

SDSNH 24679: Two immature thoracic vertebrae. Coll. R. A. Cerutti and T. A. Deméré, 2 XII 1981.

SDSNH locality 3174, H Street extension, Chula Vista:

SDSNH 24683: Adult right rib. Coll. R. A. Cerutti and B. O. Riney, 24 VIII 1982.

SDSNH locality 3175, Adams Ave., San Diego:

SDSNH 24684: Anterior end of immature left mandible. Coll. R. H. Norwood, 1975.
SDSNH 24687: Rib fragment. Coll. R. H. Norwood, 1975.

SDSNH locality 3158, Hidden Vista, Chula Vista:

SDSNH 23726: Adult braincase. Coll. R. A. Cerutti, 15 IX 1981.

SDSNH 24681: Distal ends of immature ?right radius and ulna. Coll. R. A. Cerutti, 20 VII 1981.

SDSNH 24682: Seven rib fragments. Coll. R. A. Cerutti, 22 VII 1981.

"Upper" Member.—

SDSNH locality 3173, 38th and Beech Streets, San Diego:

SDSNH 24680: Neural arch of immature thoracic vertebra (*Hydrodamalis* species indet.). Coll. T. A. Deméré, 21 I 1983.

Description of Specimens from the San Mateo Formation

Maxilla.—A juvenile left maxilla (SDSNH 21076, Fig. 2a–e), as noted by Barnes et al. (1981), is almost identical to the right maxilla (UCMP 86345) previously reported from the same locality (Domning 1978: tab. 24; pl. 17, fig. a). It is exactly the same size and represents the same growth stage, but is more complete, measuring 129 mm in overall length and 58 mm in height. (It may even represent the same individual.) The first alveolus, for a single-rooted tooth, lies slightly posterior to the zygomatic-orbital bridge and is 7.5 mm long. The second alveolus, for a two-rooted tooth, is 8.5 mm long, and the third, for a three-rooted tooth with apparently coalesced roots, is about 9 mm long and 7 mm wide. The combined length of these three alveoli is 27 mm. Posterior and dorsal to the third alveolus is a large broken dental capsule (11 mm in dorsoventral height) for an unerupted tooth. The narrowest part of the palatal surface (20 mm wide, left half only) lies just forward of the zygomatic-orbital bridge, and consists of a flat surface bordered medially by a shallow palatal gutter (containing a foramen anteriorly and ending posteriorly in another foramen) and laterally by a sharp edge where it meets the lateral surface perpendicularly. The zygomatic-orbital bridge is elevated 19 mm above the palatal surface, and is 30 mm long anteroposteriorly and 10 mm thick. The vertical plate of the bridge, which articulated with the jugal, is 55 mm in height and contacts the main body of the maxilla above the infraorbital foramen; the latter is invisible in ventral view. On the ventromedial wall of the foramen are the anterior and posterior openings of a short, horizontal canal (a continuation of the premaxillary canal); medial to the posterior opening is a larger pit or canal opening posteriorly. The palate is a maximum of 19 mm thick.

A fragmentary left maxilla of a larger juvenile (SDSNH 24413) has a palatal surface which slopes dorsolaterad just forward of the zygomatic-orbital bridge, as in more mature individuals of *Hydrodamalis*. At the level of the front side of the bridge, this surface is only 18 mm wide, proportionately narrower than in the above specimen. The lateral surface bears a prominent groove (continuation of the premaxillary canal) anterior to the infraorbital foramen. The palate reaches a thickness of 31 mm, and the intermaxillary suture bears numerous deep vertical interdigitations. No dental alveoli are preserved.

Dentition.—Teeth of *Hydrodamalis cuestae* are still unknown, but the essentially complete maxilla described above (SDSNH 21076) allows us to speculate on the homologies of the teeth present in the juvenile. The pattern of roots of the three fully erupted teeth matches that of the teeth identified as DP^{2-4} in *Dusisiren* (Domning 1978); this implies that the dental capsule contained DP^5. In view of the immediate descent of *H. cuestae* from *Dusisiren* (Domning 1978), this seems the most parsimonious interpretation. However, in living *Dugong* (Marsh 1980) and *Trichechus* (Domning 1982), the three most anterior cheek teeth of the juvenile appear to be the only premolars (DP^{3-5}). A fuller growth series of *H. cuestae* is needed to settle this question conclusively, and also to determine whether Blancan as well as Hemphillian juveniles of the species still possessed teeth.

Humerus.—An immature right humerus (SDSNH 24685, Fig. 5) is complete except for the unfused epiphyses. In size, it falls between the two immature humeri of *Hydrodamalis gigas* described by Whitmore and Gard (1977); in shape, it closely resembles

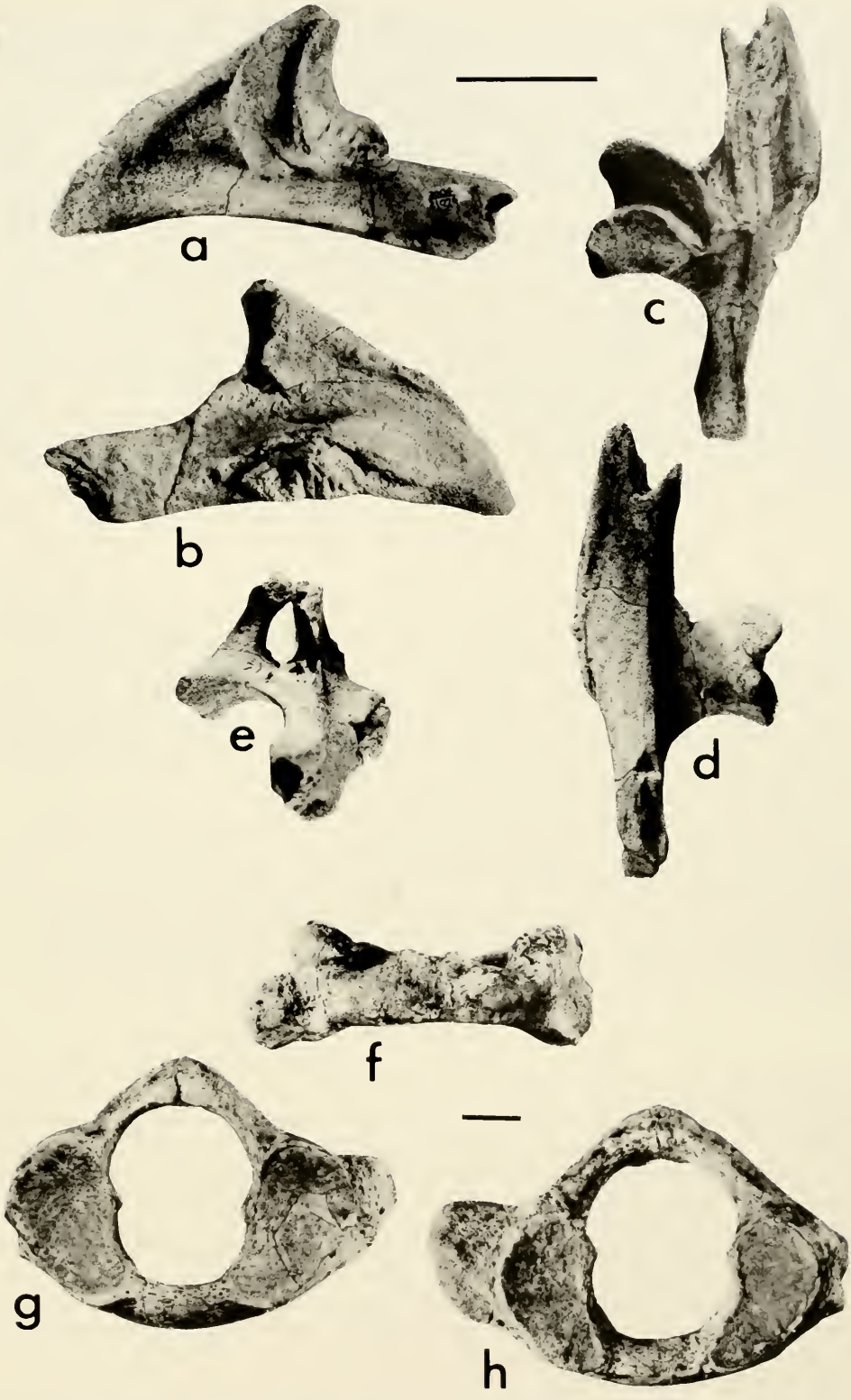

FIGURE 2. *Hydrodamalis cuestae*. a–e, juvenile left maxilla. SDSNH 21076. a, lateral view; b, medial view; c, dorsal view; d, ventral view; e, posterior view. f–h, atlas. SDSNH 23719. f, dorsal view; g, anterior view; h, posterior view. Scales = 4 cm.

TABLE 1. Skull measurements of *Hydrodamalis cuestae* (SDSNH 23726) from the San Diego Formation, in millimeters. Letters in parentheses denote measurements used by Domning (1978: tab. 2, fig. 7); e = estimated.

Rear of occipital condyles to anterior end of interfrontal suture (BI)	418e
Length of interfrontal suture	143e
Length of skull roof to rear of external occipital protuberance	310+
Top of supraoccipital to ventral side of occipital condyle (de)	223
Breadth across occipital condyles (ff')	276e
Width of supraoccipital	250
Height of supraoccipital to top of external occipital protuberance	120e
Breadth of cranium at frontoparietal suture (GG')	123
Width of foramen magnum (gg')	125e
Height of foramen magnum (hi)	64
Minimum width of basioccipital	78
Length of right zygomatic process of squamosal (O'P')	229+
Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen (O'T')	293+
Frontoparietal suture to rear of external occipital protuberance (P)	169e
Anteroposterior length of root of zygomatic process (Q'R')	103
Length of cranial portion of squamosal (S'T')	196+
Posterior height of cranial portion of squamosal (U'V')	182
Dorsoventral breadth of zygomatic process (W'X')	117

the smaller of these (USNM 186807), differing from the other (USNM 170761) in lacking a pronounced "shoulder" above the ectepicondyle. The deltoid crest is massive and rounded, without a recurved flange. The total length (without epiphyses) is 291 mm; the proximal breadth, 130 mm; and the distal breadth, 156 mm.

Ulna.—The proximal end of a juvenile ?right ulna (SDSNH 24686) has a width of 65 mm; the shaft is thicker anteroposteriorly than mediolaterally. It compares well in proportions with the ulna of a much larger immature *H. gigas* (USNM 170761) from Amchitka (Whitmore and Gard 1977:pl. 8, figs. 3–5).

Ribs.—The proximal end of a subadult right rib (SDSNH 22655) is very flat (65 × 34 mm) and has a tiny tubercle whose lateral edge is 74 mm from the tip of the capitulum. The distal end of an immature rib (SDSNH 24454) measures 59 × 54 mm in diameter and has a broad, concave, rugose distal surface for cartilage attachment. A zone of cancellous bone is partly exposed by bone resorption on its medial side. The proximal end of a larger, more posterior left rib (SDSNH 23384) has the capitulum and tubercle coalesced. Both it and SDSNH 22655 are completely dense where broken.

Description of Specimens from the San Diego Formation

Skull.—A nearly complete adult braincase (SDSNH 23726, Fig. 6, Table 1), including the right zygomatic process of the squamosal but lacking the pterygoid processes, expands our knowledge of the occipital region of *Hydrodamalis cuestae.* The interior, however, is still filled with very hard matrix, precluding examination of the internal structures. The dimensions of the preserved portions indicate that this individual was larger than any other *Hydrodamalis* or other sirenian ever found, and in life no doubt measured well over 10 m in body length.

Frontal: The supraorbital processes are missing, but the anterior border seems to be complete. It is arched upward somewhat at the midline, due to a broad, prominent median boss on the dorsal surface. Lateral to this are depressions bordered by upraised forward extensions of the temporal crests. The lateral surfaces drop almost perpendicularly from these crests, with little or no overhang.

Parietal: The cranial vault is square anteriorly with no overhang of the temporal crests, which are nearly parallel anteriorly but posteriorly form sharp ridges which diverge and descend to meet the dorsal ends of the sigmoid ridges of the squamosals. There is only a slight indentation in the dorsal surface where it meets the top of the

squamosal, much as in *H. gigas*. The parietal roof is slightly concave anteriorly and flat posteriorly.

Supraoccipital: The width/height ratio is 2.08, being within the previously reported range of variation. The supraoccipital forms an angle of 124° with the after part of the parietal roof and is within the range of variation of the USNM sample of Bering Island *H. gigas*. The external occipital protuberance is low and indistinct, with no median ridge extending below it. The lateral borders are rounded, rugose, and extremely thick and massive.

Exoccipital: The sutures with the supraoccipital are indistinct, but the exoccipitals apparently fail to meet in the dorsal midline. The dorsal border of the foramen magnum is very gently arched with almost no dorsal peak, as in *H. gigas*. The dorsolateral border of the exoccipital is very thick, rounded, and rugose, and overhangs posteriorly, but is not expanded to the degree seen in *H. gigas*. However, it does confirm the supposition (Domning 1978) that the thin exoccipital border seen in the holotype of *H. cuestae* (UCMP 86433) is abnormal for the species. The paroccipital process is massive and rugose. The occipital condyle is very large and broad, and projects well abaft the occiput. Its upper part curves forward only slightly and there is no supracondylar fossa, again confirming the abnormality of the holotype. The condyle measures 78 mm in width and 117 mm front to back, a ratio of 0.67 (intermediate between values reported for *Dusisiren* and *H. gigas* by Domning 1978).

Basioccipital: Completely fused with basisphenoid and exoccipitals, indicating adulthood.

Basisphenoid: Largely removed by bulldozer, but originally much thicker than in the (abnormal) holotype.

Squamosal: The sigmoid ridge is about as reduced as in *H. gigas,* and is invisible in posterior view. The cranial portion dorsal to the zygomatic root is very slightly concave, as in the holotype. There is a protuberance about 1 cm high just above the external auditory meatus, an individual peculiarity not observed in the related forms. The temporal condyle is broad, smooth, and not distinctly demarcated; the postarticular fossa is broad and well developed; and the postglenoid process is about 2 cm high and very robust, unlike *H. gigas*. The processus retroversus is straight and very prominent, with a deep posterior indentation as in the holotype. The posterodorsal edge of the zygomatic process is damaged, giving the process a more lozenge-shaped outline than it originally had; it may have approached that of *H. gigas* in convexity. The forward end of the process is missing; its lateral edge was sharper than its medial. Its underside bears a clear impression for the zygomatic process of the jugal, which extended back almost to the level of the forward edge of the zygomatic root. Just posterior to the tip of the jugal is a large smooth convexity not so prominent in other *Hydrodamalis* specimens.

Periotic: Present on right side but not prepared.

Tympanic: A fragment is present on the right side, just posterior to the auditory meatus.

Mandible.—The anterior end of an immature left mandible (SDSNH 24684), badly worn, shows a *H. gigas*-like convex outline of the anteroventral border. The mental foramen appears to have lain well forward (at the level of the symphysis), as assumed for the holotype of *H. cuestae*.

Vertebrae.—Ten of the anterior vertebrae are known from SDSNH 23719, an individual smaller than SDSNH 23726. Partial thoracics from other animals (SDSNH 24679, 24680) are also available.

Atlas (Fig. 2f–h, Table 2): The upper arch lacks a keel and articular surface for the axis, but has an anterior median notch flanked by a pair of rugose protuberances, and is penetrated posteriorly by a vertical canal about 4 mm wide. The canal for the first cervical nerve atop each cotyle is deep but not bridged by bone. A possible vestige of a vertebral arterial canal on each side, filled with matrix, may not have been patent; in any case there is no distinct notch on the transverse process as in *Dusisiren jordani*.

Axis (Fig. 3a–c, Table 3): The odontoid process bears a broad, smooth, saddle-

TABLE 2. Measurements of atlas of *Hydrodamalis cuestae* (SDSNH 23719) from the San Diego Formation, in millimeters; e = estimated.

External height	181
Internal height	115
Total breadth	292e
Width between tips of processes for transverse ligament	78
Breadth across anterior cotyles	219
Breadth across posterior cotyles	190
Length in dorsal midline	42
Length in ventral midline	49

TABLE 3. Measurements of axis of *Hydrodamalis cuestae* (SDSNH 23719) from the San Diego Formation, in millimeters; e = estimated.

Total height	196+
Tip of odontoid process to rear of centrum	102
Breadth across cotyles	182
Breadth of cotyle	54
Height of cotyle	85
Posterior breadth of centrum	116
Posterior height of centrum	71
Width of neural canal	88
Height of neural canal	95e
Breadth across postzygapophyses	167

TABLE 4. Measurements of cervical and thoracic vertebrae of *Hydrodamalis cuestae* (SDSNH 23719) from the San Diego Formation, in millimeters; e = estimated; a = asymmetrical.

	C6	C7	T1	?T2	?T3	?T4	?T5	?T6
Total height	180	206	219+	···	···	···	···	···
Breadth across transverse processes	306e	355a	···	···	344+	345+	354	···
Anterior breadth of centrum	126	135	132	···	125	137	153	160
Posterior breadth of centrum	131	123	128	···	137	156	161e	165
Height of centrum in midline	82	81	76	81	79	95	97	100
Thickness of centrum in midline	33	38	56	69	69	71	75	77
Width of neural canal	124	120	131	···	119	116	116	112
Height of neural canal	81	81	91	···	···	81	81	93
Breadth across prezygapophyses	···	249	240e	···	240e	173e	170e	···
Breadth across postzygapophyses	···	···	218	···	···	169	178	···
Length from front of prezygapophysis to rear of postzygapophysis	58	72	76	···	82+	105e	110e	···

shaped articular surface ventrally. The vertebral arterial canal is broadly open as in the holotype. The neural spine is not preserved.

Cervicals 6–7 (Fig. 3d–e, Table 4): The vertebral arterial canal is large in C6 and on the right side of C7, but open laterally on the left side, which lacks the fused cervical rib; an anterior demifacet and a tubercular articulation, apparently for the cervical rib, are present. A similar asymmetry was observed in one *D. jordani* vertebra (Domning 1978:pl. 9, fig. h). The transverse process of C6 juts farther laterad than in the corresponding vertebra of *D. jordani.*

Thoracics 1–?6 (Fig. 3f–g, 4, Table 4): The anterior thoracic centra have square sagittal sections like *H. gigas* and unlike the holotype, and sieve-like epiphyses as in the Recent species. The neural arch of T1 does not have "shoulders" like *D. jordani*

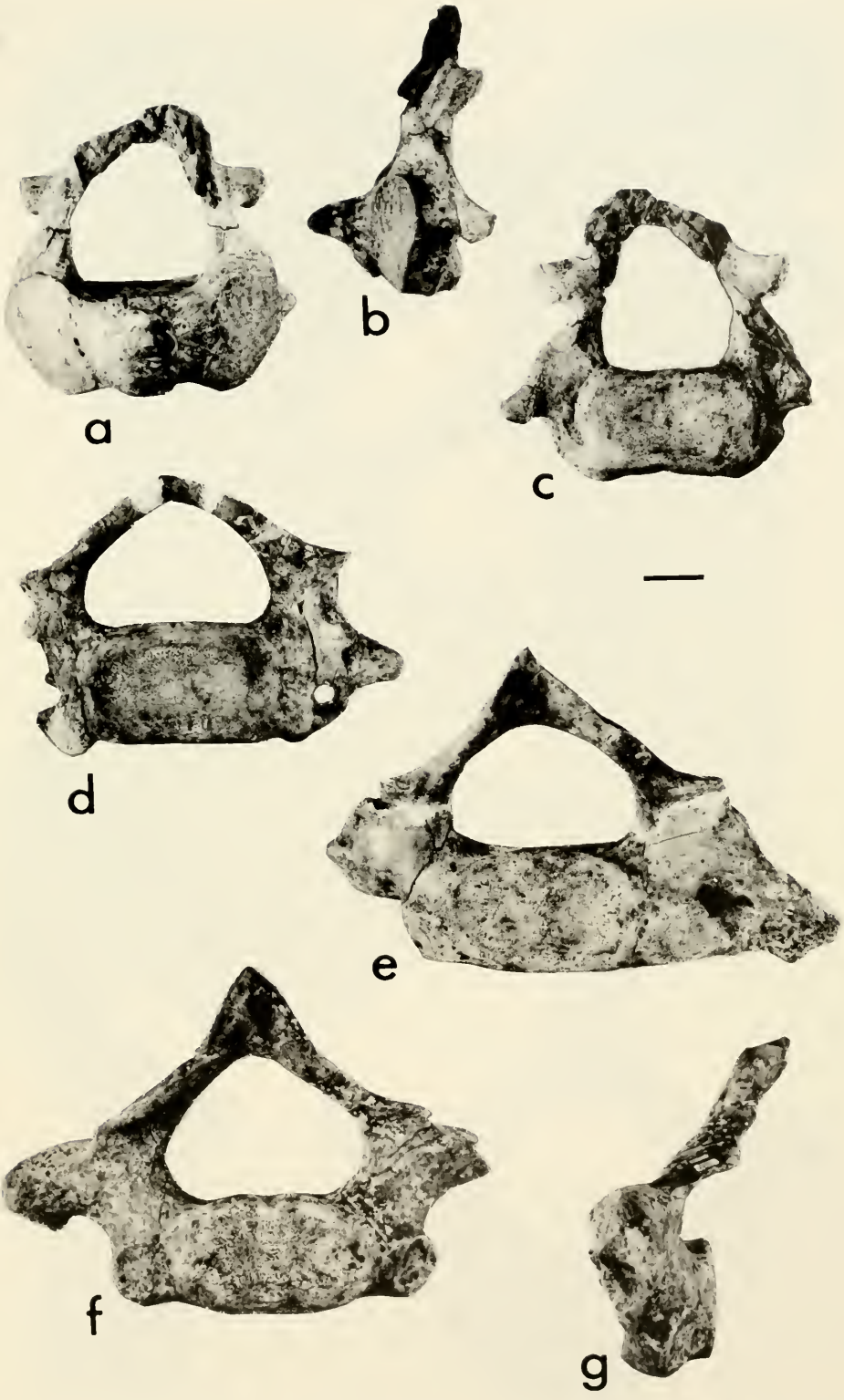

FIGURE 3. *Hydrodamalis cuestae.* Vertebrae. SDSNH 23719. a–c, axis. a, anterior view; b, lateral view; c, posterior view; d, C6, posterior view; e, C7, posterior view. f–g, T1. f, posterior view; g, lateral view. Scale = 4 cm.

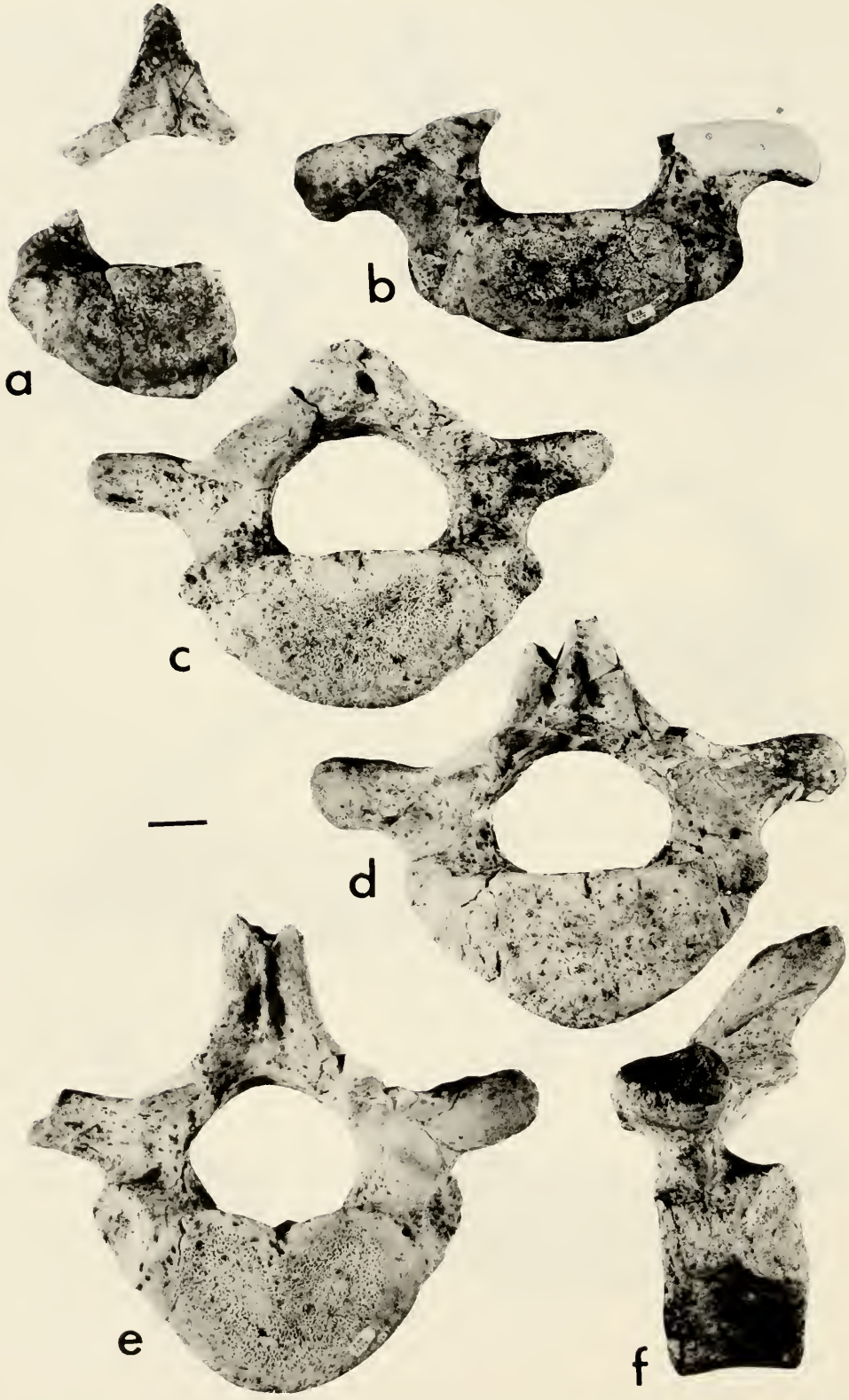

FIGURE 4. *Hydrodamalis cuestae.* thoracic vertebrae. SDSNH 23719. Posterior views: a, ?T2; b, ?T3; c, ?T4; d, ?T5; e, ?T6. f, ?T6, lateral view. Scale = 4 cm.

FIGURE 5. *Hydrodamalis cuestae.* Immature right humerus. SDSNH 24685. a, anterior view; b, medial view. Scale = 4 cm.

or the holotype. The protuberances for semispinalis tendons are indistinct. The neural spines are inclined backward and are much thicker posteriorly than at their anterior edges, in the manner of *H. gigas* rather than *Dusisiren.* The posterior sides of the spines are concave with distinct median ridges. The apices of the neural canals are not slit-like. SDSNH 24680, a partial neural arch, represents an immature animal and was apparently not fused to its centrum. A poorly preserved pair of thoracic vertebrae with arches and centra unfused (SDSNH 24679) represents a still younger animal; the maximum breadth of one of these centra is 127 mm, and its thickness is 48 mm.

Ribs.—One nearly complete right adult rib (SDSNH 24683, Fig. 7a) and several fragmentary ones (SDSNH 21685, 24682, 24687) have been recovered from the San Diego Formation. SDSNH 24683 is from near the middle of the thorax; it lacks the capitulum, but would have measured about 1002 mm in total straight-line length. At

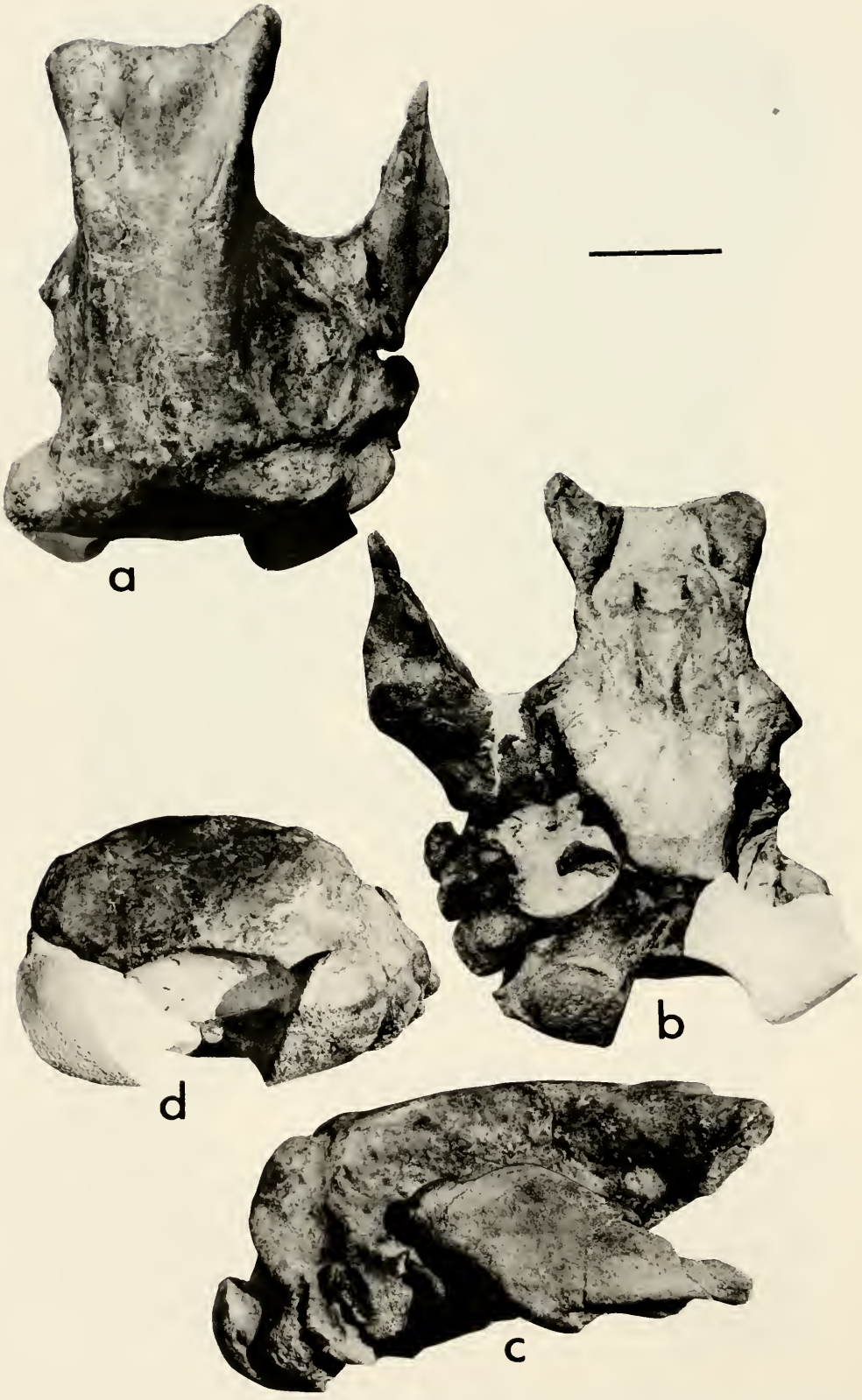

FIGURE 6. *Hydrodamalis cuestae*. Adult braincase, SDSNH 23726. a, dorsal view; b, ventral view; c, lateral view; d, posterior view. Left occipital condyle restored. Scale = 10 cm.

FIGURE 7. *Hydrodamalis cuestae*. a, adult right rib. SDSNH 24683. Scale = 10 cm. b, immature distal ?right radius and ulna, ?medial view. SDSNH 24681. Scale in cm.

the middle of the shaft it measures 88 × 68 mm; the distal end is swollen to 98 × 78 mm, and slightly swept back. The distal tip bears an oval rugose concavity, and there is no well-marked angle. There is also no zone of cancellous bone visible on the medial surface. SDSNH 24682 (seven associated adult rib fragments) includes a damaged proximal end and two complete distal ends; the latter taper more gradually than SDSNH 24683 and are more flattened mediolaterally (90× 39 mm, 25 cm from distal end of one fragment). Except for the proximal end and another fragment of a distal tip, these fragments are all composed wholly of dense bone. Another fragment (SDSNH 24687) from the middle of a large rib (92 × 72 mm) has a large zone of cancellous bone just beginning to crop out on its medial side.

Radius-ulna.—SDSNH 24681 (Fig. 7b) comprises the distal ?right radius and ulna of an immature animal, lacking the epiphyses. The shaft of the radius is flattened anteroposteriorly (about 60 × 40 mm) and is concave both mediolaterally and proximodistally on its posterior surface; it is also slightly bowed (concave ?medially). Its distal end is expanded to a width of 78 mm and an anteroposterior thickness of 75 mm, with a flat posterior surface. The anterior surface bears three low, irregular knobs about 1.5, 4, and 10 cm, respectively, from the distal end. The shaft of the ulna is compressed mediolaterally and markedly bowed (concave posteriorly); its expanded distal end measures 71 mm mediolaterally and an estimated 75–80 mm anteroposteriorly, with a flat anterior surface. The distal thickness from the anterior side of the radius to the posterior side of the ulna, allowing for the interosseous space whose width is indicated by fragments of matrix, was about 155 mm.

Discussion

The specimens herein described are distinguished from *Dusisiren* Domning 1978 by the following derived characters: In the case of those from the San Mateo Formation, their large adult size, reduced juvenile dentition, and invisibility of the infraorbital foramen in ventral view; in the case of those from the San Diego Formation, their large size, lack of a dorsal peak to the foramen magnum, reduced sigmoid ridge on the squamosal, lack of a dorsal articulation between the atlas and axis, stouter and more posteriorly inclined thoracic neural spines, presence of a core of cancellous bone in immature ribs, and greater curvature of the ulna. Primitive characters of these specimens separating them from *Hydrodamalis gigas* include: A square cranial vault with more distinct temporal crests, less expanded occipital borders, a posteriorly notched zygomatic root, a large postglenoid process, a more anteriorly located mental foramen, and retention of teeth in the juvenile (at least in the Hemphillian specimens). In some details (zygomatic process possibly with rounded posterior end, thoracic centra square in sagittal section, first thoracic neural arch without "shoulders") the new specimens from the San Diego Formation are more derived than previously known *H. cuestae,* while in another respect (well-developed postarticular fossa of squamosal) they are more primitive. However, such characters may be expected to vary from more "primitive" to more "derived" conditions in a single population at any given time. In most respects the new specimens most closely resemble the previously described specimens of *H. cuestae.* They are, accordingly, referred to that species, with the possible exception of the fragmentary vertebra (SDSNH 24680) from the highest unit, which is best regarded as *Hydrodamalis* species indet.

Conclusions reached earlier by Domning (1978) are supported by the new material:

1. The holotype of *H. cuestae* is abnormal in degree of development of the exoccipital border, supracondylar fossa, and basisphenoid. The skull from the San Diego Formation shows the conditions expected in a form phylogenetically intermediate between *D. jordani* and *H. gigas.*
2. *Hydrodamalis* grew larger in the southern parts of its range than in the marginal habitat of the Commander Islands. The San Diego skull is the largest of any individual *Hydrodamalis* or other sirenian ever discovered, and several postcranial elements also appear to set new size records.

Additional conclusions are permitted by the new material:

1. The sirenian present in the San Diego Formation is indeed *H. cuestae,* as would be predicted from the age of the unit.
2. Hemphillian-aged juveniles of *H. cuestae* possessed at least four upper teeth, probably DP^{2-5}.

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Literature Cited

Barnes, L. G. 1973. Pliocene cetaceans of the San Diego Formation, San Diego, California. pp. 37–42 *in* A. Ross and R. J. Dowlen (eds.). Studies on the geology and geologic hazards of the greater San Diego area, California. San Diego Association of Geologists.

———. 1976. Outline of eastern North Pacific fossil cetacean assemblages. Systematic Zoology 25(4):321–343.

———, H. Howard, J. H. Hutchison, and B. J. Welton. 1981. The vertebrate fossils of the marine Cenozoic San Mateo Formation at Oceanside, California. pp. 53–70 *in* P. L. Abbott and S. O'Dunn (eds.). Geologic investigations of the coastal plain, San Diego County, California. San Diego Association of Geologists.

Deméré, T. A. 1983. The Neogene San Diego Basin: A review of the marine Pliocene San Diego Formation. pp. 187–195 *in* D. K. Larue and R. J. Steel (eds.). Cenozoic marine sedimentation, Pacific margin, U.S.A. Society of Economic Paleontologists and Mineralogists.

Domning, D. P. 1978. Sirenian evolution in the North Pacific Ocean. University of California Publications in Geological Sciences 118:1–176.

———. 1982. Evolution of manatees: A speculative history. Journal of Paleontology 56(3): 599–619.

Ehlig, E. L. 1979. Miocene stratigraphy and depositional environments of the San Onofre area and their tectonic significance. pp. 43–51 *in* C. J. Stuart (ed.). Miocene Lithofacies and Depositional Environments, Coastal Southern California and Northwestern Baja California. Society of Economic Paleontologists and Mineralogists.

Grant, U. S., IV, and H. R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. San Diego Society of Natural History Memoir 1: 1–1036.

Hertlein, L. G., and U. S. Grant, IV. 1944. The geology and paleontology of the marine Pliocene of San Diego, California, Pt. 1, Geology. San Diego Society of Natural History Memoir 2:1–72.

——— and ———. 1960. The geology and paleontology of the marine Pliocene of San Diego, California, Pt. 2a, Paleontology. San Diego Society of Natural History Memoir 2a:73–133.

——— and ———. 1972. The geology and paleontology of the marine Pliocene of San Diego, California, Pt. 2b, Paleontology. San Diego Society of Natural History Memoir 2b:143–409.

Howard, H. 1949. New avian records for the Pliocene of California. Carnegie Institution of Washington Publication 584:177–199.

———. 1971. Pliocene avian remains from Baja California. Los Angeles County Museum Contributions to Science 217:1–17.

———. 1976. A new species of flightless auk from the Miocene of California (Alcidae: Mancallinae). pp. 141–146 *in* S. L. Olson (ed.). Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. Smithsonian Contributions to Paleobiology 27.

———. 1978. Late Miocene birds from Orange County, California. Natural History Museum of Los Angeles County Contributions in Science 290:1–26.

———. 1982. Fossil birds from Tertiary marine beds at Oceanside, San Diego County, California, with descriptions of two new species of the genera *Uria* and *Cepphus* (Aves: Alcidae). Natural History Museum of Los Angeles County Contributions in Science 341:1–15.

Ingle, J. C., Jr. 1967. Foraminiferal biofacies, variations and the Miocene–Pliocene boundary in southern California. Bulletins of American Paleontology 52(236):216–394.

Keen, A. M., and H. Bentson. 1944. Check list of California Tertiary marine Mollusca. Geological Society of America Special Paper 56:1–280.

Mandel, D. J., Jr. 1973. Latest Pliocene Foraminifera in the upper part of the San Diego Formation, California. pp. 33–36 *in* A. Ross and R. J. Dowlen (eds.). Studies on the geology and geologic hazards of the greater San Diego area, California. San Diego Association of Geologists.

Marsh, H. 1980. Age determination of the dugong (*Dugong dugon* (Müller)) in northern Australia and its biological implications. pp. 181–201 *in* W. F. Perrin and A. C. Myrick, Jr. (eds.). Age determination of toothed whales and sirenians. Reports of the International Whaling Commission, Special Issue No. 3.

Miller, L. 1956. A collection of bird remains from the Pliocene of San Diego, California. Pro-

ceedings of the California Academy of Science 28(16):615–621.

Moyle, W. R., Jr. 1973. Geologic map of western part of Camp Pendleton, southern California. U.S. Geological Survey Open File Map, Scale 1:48 000.

Repenning, C. A., and R. H. Tedford. 1977. Otarioid seals of the Neogene. U.S. Geological Survey Professional Paper 992:1–93.

Vedder, J. G. 1972. Review of stratigraphic names and megafaunal correlation of Pliocene rocks along the southeast margin of the Los Angeles basin, California. pp. 158–172 *in* E. H. Stinemeyer (ed.). Pacific Coast Miocene Biostratigraphic Symposium. Society of Economic Paleontologists and Mineralogists.

Webb, S. D., B. J. MacFadden, and J. A. Baskin. 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. American Journal of Science 281:513–544.

Whitmore, F. C., Jr., and L. M. Gard, Jr. 1977. Steller's sea cow (*Hydrodamalis gigas*) of Late Pleistocene age from Amchitka, Aleutian Islands, Alaska. U.S. Geological Survey Professional Paper 1036:1–19.

Woodford, A. O. 1925. The San Onofre Breccia, its nature and origin. University of California Publications in Geological Sciences 15:159–280.

Woodring, W. P., and M. N. Bramlette. 1950. Geology and paleontology of the Santa Maria district, California. U.S. Geological Survey Professional Paper 222:1–185.

Young, J. M., and R. W. Berry. 1981. Tertiary lithostratigraphic variations, Santa Margarita River to Aqua Hedionda Lagoon. pp. 33–51 *in* P. L. Abbott and S. O'Dunn (eds.). Geologic investigations of the coastal plain, San Diego County, California. San Diego Association of Geologists.

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Fossil Syncarida

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Abstract. All known fossil syncaridans are reviewed, and their family level taxonomy revised to form a more natural system. One anaspidid anaspidacean is known, *Anaspidites antiquus* (Chilton), from the Triassic of Australia. The northern hemisphere Paleozoic Palaeocaridacea are sorted into four families: Minicarididae (*Minicaris brandi* Schram, *Erythrogaulos carrizoensis* new genus, new species), Acanthotelsonidae (*Acanthotelson stimpsoni* Meek & Worthen, *A. kentuckiensis* new species, *Uronectes fimbriatus* (Jordan), *U. kinniensis* Schram & Schram, *Palaeosyncaris dakotensis* Brooks, *P. micra* new species), Palaeocarididae (*Palaeocaris typus* Meek & Worthen, *P. retractata* Calman, *P. secretanae* new species), and Squillitidae (*Squillites spinosus* Scott, *Praeanaspides praecursor* Woodward, *Nectotelson krejcii* (Fritsch)). Several taxa are too incompletely known to be placed with certainty at this time within these families: *Pleurocaris annulatus* Calman, *Williamocalmania vandergrachti* (Pruvost), *Brooksyncaris canadensis* (Brooks), *Palaeorchestia parellela* (Fritsch), and *Clarkecaris brasilicus* (Clarke). An analysis of phylogenetic relationships of syncaridan families is presented.

Introduction

It is a historical curiosity that syncarids were known as fossils 45 years before they were discovered living in Tasmania. The understanding of their relationship to other eumalacostracans has unfolded only gradually, and is still not completely resolved (see e.g., Dahl 1983; Hessler 1983; Schram 1981*c*, 1984; Watling 1981, 1983). The syncarids remain one of the most singularly interesting groups within the Eumalacostraca.

The first syncarid, a Permian fossil, was described by Jordan (1847) as *Gampsonyx fimbriatus* (now known as *Uronectes fimbriatus*). The species was immediately recognized by Jordan as unusual, though he compared it to amphipods in terms of its general form. The question of its exact systematic position, however, could not be definitively resolved, as evinced by Burmeister (1855) who, in a detailed consideration of the beast, made passing mention of possible stomatopod *and* amphipod similarities. Burmeister remarked that its closest affinities seemed to be with schizopods, yet concluded it was an example of a singular group ("sie ist vielmehr der Repräsentiert einer besondern Gruppe," p. 200). Roemer (1856) had no such reservations and placed this species within the Stomatopoda.

Subsequently, Meek and Worthen (1865) described 2 more "syncarid" species, *Acanthotelson stimpsoni* and *Palaeocaris typus*, and placed them within the Isopoda.

Fritsch (1870) described what he thought was a species related to *G. fimbriatus*, which he called *Gampsonychus krejcii*. Fritsch (1876) also described what he thought was yet another species of "*Gampsonychus*," which was later placed by Zittel (1885) in a separate genus, *Palaeorchestia parallela*.

It was Packard (1885, 1886*a*) who finally recognized in part the separate status of these fossils, and erected the taxon Syncarida. However, he placed only *A. stimpsoni* within this new group. He then proceeded to compare "*Gampsonyx*" with *Palaeocaris typus*, and concluded that these latter taxa served ". . . to bridge over the chasm existing between the thoracostracous suborders, Syncarida and Schizopoda . . .," (Packard 1886*a*: 129).

When Thompson (1893, 1894) described the living species *Anaspides tasmaniae* he placed it in a separate family of the Schizopoda. However, it was Calman (1896) who realized the relationship of *Anaspides* to the various fossil forms and united them altogether in the Syncarida, which he later (1904) elevated to superorder status within the Eumalacostraca. This arrangement completely overshadowed Grobben's (1919) attempt to erect a subdivision Anomostraca within the Malacostraca for *Anaspides.*

As if to celebrate this apparent resolution of syncarid affinities, a whole host of new fossil species soon entered the literature: *Praeanaspides praecursor* Woodward, 1908; *Pleurocaris annulatus* Calman, 1911; *Anaspides brasilicus* Clarke, 1920; *Palaeocaris vandergrachti* Pruvost, 1922; *Anaspides antiquus* Chilton, 1929; *Palaeocaris retractata* Calman, 1932 (actually known since 1911); and *Squillites spinosus* Scott, 1938 (a name which mistakenly resurrected the idea of supposed affinities to stomatopods).

The taxonomy of the group then achieved a certain degree of stability until Brooks (1962*a, b*) recognized distinct generic status for *Anaspidites antiquus* and *Clarkecaris brasilicus* from *Anaspides,* and also recognized at that time the separate status of the Paleozoic taxa with his order Palaeocaridacea. Brooks (1962*b*) went on to describe a new species, *Palaeosyncaris dakotensis,* but mistakenly synonymized (Brooks 1969) most of the, until then separate, Palaeozoic genera with the genus *Palaeocaris.*

A major revision of the fossil syncarids began with a redescription of *Squillites spinosus* by Schram and Schram (1974). Schram (1979*a*) continued this review by reestablishing the separate generic status of several of the Paleozoic taxa, at least for the British Carboniferous fauna, as well as describing the earliest syncarid, *Minicaris brandi.* A second species of *Uronectes, U. kiniensis,* was described by Schram and Schram (1979). The work herein completes this revision, and examines all the known fossil syncarids. In addition to reestablishing as valid some old generic names, 4 new species are described, and 3 new genera are recognized. The artificial familial arrangement of Brooks (1962*a*) is essentially discarded and a new classification of the Paleozoic families is put forth, one which is felt to be more natural.

Abbreviations

Prefixes of catalog numbers for various institutions are as follows:

AM	Museum d'Histoire Naturelle, Autun, France
B	Museum d'Histoire Naturelle, Paris, France
BS	Bayerisches Staatssamlungen für Paläontologie und historisches Geologie, Munich, West Germany
CGH	Národni Museum, Prague, Czechoslovakia
F	Australian Museum, Sydney, New South Wales
GSE	Institute of Geological Sciences, Edinburgh, Scotland
GSL	Institute of Geological Sciences, Leeds, England
I, In	British Museum (Natural History), London, England
ISGS	Illinois State Geological Survey, Urbana, Illinois
Jk	Museum für Naturkunde (Janensch Catalog), Berlin, East Germany
M, Me	Národni Museum, Prague, Czechoslovakia
NB	Rijks Geololgische Dienst, Heerlen, The Netherlands
NYSM	New York State Museum, Albany, New York
PE	Field Museum of Natural History, Chicago, Illinois
PMB	Museum für Naturkunde (Paleontologisches Museum Catalog), Berlin, East Germany
SDSNH	San Diego Natural History Museum, San Diego, California
US	University of Sydney, Paleontology Collection, Sydney, New South Wales
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
X	University of Illinois, Paleontology Collection, Urbana, Illinois
YPM	Yale Peabody Museum of Natural History, New Haven, Connecticut

Living Anaspidacea

In 1980 I was able to collect and study several species of living anaspidaceans in Tasmania with the assistance of the staff of the University of Tasmania. Several of these observations have not been recorded before, and offer some insights into the biology of the fossil syncarids.

The most widely dispersed anaspidacean is *Anaspides tasmaniae* (a rather variable taxon which will probably contain several subspecies—R. Swain, *personal communication*) which occur in streams, lakes, and caves widely scattered about the island of Tasmania. The animals are in constant motion, somewhat less so in the wild than in the laboratory. They tend to engage in a constant and random patrol of their pools. They seem to ignore each other, and in the laboratory they climb over each other in the course of their wanderings like any other obstacle in their path. The exopods constantly vibrate anteriorly to posteriorly, moving the epipodites in the process. The annulate pleopods are directed ventro-laterally, and push the body along the bottom in metachronal rhythm with the thoracic endopods. While collecting *Anaspides,* some inadvertently fell out of the dip net onto the ground, whereupon they righted themselves and commenced to explore their terrestrial environs with ease. Richardson (*personal communication*) relates that occasionally, albeit rarely, they are naturally encountered out of their pools on land. This species does not swim at all well. When startled they will execute a single caridoid flexure that propels them up into the water column. However, they then drift passively until gravity returns them to the bottom. This probably accounts for their inability to survive in areas where European sport fish have been introduced, and also makes it extremely easy to collect them. Overall, *A. tasmaniae* is a very alert animal. The flagellae of both sets of antennae orient in different directions and constantly sweep about. They are omnivorous, prefering to scavenge, and are also known to pick up large sand grains and manipulate them with their mouthparts, apparently to scrape them of organics.

Paranaspides lacustris is a smaller animal than *A. tasmaniae,* and exhibits some distinctly different behavior. Their pleopods also function like those of *Anaspides* when they walk on the bottom. However, *Paranaspides* seems to be much more versatile in its locomotion. When startled they may execute the single caridoid flexure already mentioned, or they may dart away in some direction parallel to the bottom, or they may lay quite still. When they do enter the water column they are capable of swimming quite well. *Paranaspides* was observed by me to swim for hours near the surface in a small thermos-container. In the laboratory, they were generally less active animals than *Anaspides.* Although they have a flexure point in the abdomen to facilitate the caridoid reaction, when they rest in their habitat on the bottom ooze or on the water plants they prefer, they reflex and hold the tailfan dorsad off the substrate.

Allanaspides is the smallest of the Anaspididae. *A. helionomus* is collected from yabbie (crayfish) burrows. Unlike the 2 species above, *A. helionomus* does not beat its exopods in a simple to-and-fro pattern, but seems to rotate them. The exact manner is not clear, but the resultant current sucks water under the head of the animal and back towards the tail. Small, young individuals do not beat their exopods when at rest; only the adult animals do. The anterior thoracopods are oriented anteriorly under the head while at rest; in combination with the described current they may function in filter feeding. Also, unlike *Anaspides* and *Paranaspides, Allanaspides helionomus* uses its pleopods in a somewhat different manner. The uniramous annulate abdominal appendages are held rigid and each pair is oriented in a different direction. When they assist in walking they push off the bottom like oars using just their tips. Walking in *A. helionomus* is best described as a "scurrying crawl," occurring in intermittent bursts of activity. When at rest, the first 2 pleopods vibrate vigorously to aerate the fleshy thoracic epipodites. *Allanaspides* swims very well, and was observed to do so even upside down. The animals may be detritovores since in the laboratory they were observed to fondle fecal pellets with their mouthparts. The burrows these animals live in occur in grass marshes on surfaces of gentle slope, affording a modicum of drainage and no long-standing water.

Micraspides calmani possess a very flexible body, easily achieving flexion dorsally and ventrally as well as considerable lateral bend, and is the most infaunal of any of the species observed by me in Tasmania. It also lives in pools and yabbie burrows in grass swamps, but seems to better tolerate conditions with poorer drainage than do species of *Allanaspides*. *Micraspides* moves with bursts of intermittent scurrying, reminiscent of that seen in some centipedes. The annulate pleopods are held somewhat stiffly, and operate only within the metachronal sequence of all the limbs, thus differing only in form and not function from the thoracopods. When not moving they do not move any of the appendage parts. No caridoid escape reaction could be elicited from *Micraspides*; when startled or prodded the animals would take evasive action by turning laterally or flexing ventrally, eventually to change their direction of movement 180°. They are thus ideally adapted to climbing in, around, over, under, and through obstacles in the vegetation-choked, muddy habitats they prefer.

Several aspects of the above have direct bearing on interpretation of the fossils. The annulate pleopods seen on the living forms are noted as one of the most versatile and important aspects of the anatomy of these creatures; serving to achieve walking, swimming, and ventilation of epipodites. They also form, for the most part, a functional continuum with the thoracopods (MacMillan et al. 1981). This has great bearing on the Paleozoic fossils, which were once mistakenly thought (Brooks 1962*b*) to all have flap-like pleopods and thoracic exopods. The functional system for pleopods seen in the living forms is quite distinct from what might be postulated for those few paleocaridaceans with biramous flap-like pleopods, which would appear to have been capable of only one action, a to-and-fro vibration on the ventral side of the abdomen. Such limbs would serve in swimming, but have little or no effect on walking on the bottom or producing ventilatory currents over the thoracic epipodites. The latter would have to be achieved by the vibration of the flap-like thoracic exopods. In turn, the exopods, because of their form and consequent limitation of movement, could not serve to generate potential filtering currents around the body as do the rotatory exopod movements of a form like *Allanaspides*.

Palaeocaridaceans such as the acanthotelsonids, or in part the palaeocaridids, probably exhibited a functional system not unlike that seen in other eumalacostracan groups, such as mysidaceans, euphausiaceans, and natant decapods, wherein the pleopods are the sole or primary organs of swimming in the adult stage. The system seen in the anaspidaceans, the squillitids, and in part the palaeocaridids would then appear to possibly represent a functional advance in which the entire trunk appendage series is capable of acting as a coordinated unit. In this respect, it seems to have been a successful enough arrangement of parts to have perhaps evolved at least twice within the syncarids: once in the palaeocaridid/squillitid line and again in the anaspidaceans.

Some interesting questions arise for which, at the present, there are no obvious answers. In those living eumalacostracans for which the use of pleopods for swimming is well developed there has evolved an excellent caridoid escape reaction. Does the existence of a similar anatomical system in some of the Palaeocaridacea mean that they too may have had a well-developed caridoid escape reaction, in contrast to the rather inefficient single-flexure behavior seen in living anaspidaceans? Dahl (1983) suggests that the caridoid escape reaction of eumalacostracans was independently evolved in mysidaceans and natant eucarids. Does its possible existence in some palaeocaridaceans mean there was a third independent evolution of this behavior, or is its possible presence in the syncarids an argument for the caridoid escape reaction being considered as a derived character applicable to all eumalacostracans (Hessler 1983) and which has merely been repeatedly lost? Do these functional considerations tell us anything about character polarities (see next section) within syncarids? If the integrated system with annulate appendage parts represents a functional advance within the syncarid line, this might indicate that the purely flap-like structures are primitive and that animals which possess them are closer to the stem-group. Thus bathynellaceans and many of the palaeocaridaceans might be considered more primitive than anaspidaceans. On the other hand, if annulate limb parts and a functionally integrated trunk might represent

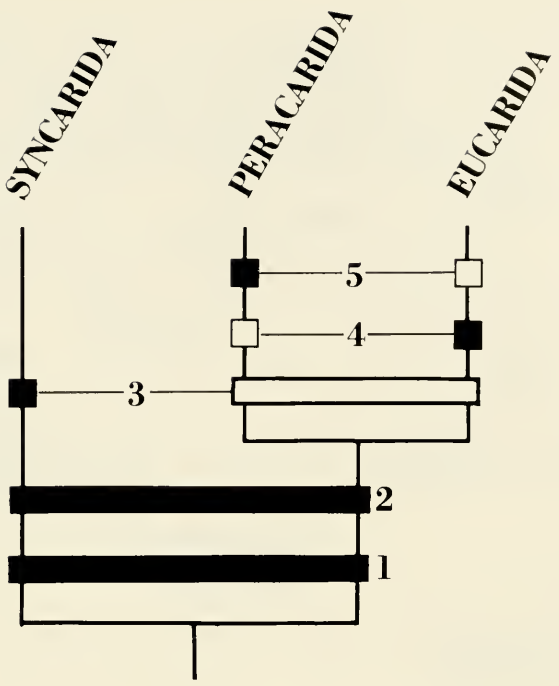


FIGURE 1. Classical arrangement of the superorders of Eumalacostraca *sensu stricto*. Derived characters are: 1) caridoid escape reaction (and its associated features of abdominal specializations, *see* Hessler 1983), 2) antennal scale of a single joint, 3) loss of a carapace, 4) carapace fused to thoracomeres, and 5) oöstegite brood pouch.

an advance for syncarids, another scenario is possible. There is a tendency for paedomorphosis in syncarids (reduced or absent posterior limbs, small body size, free first thoracomere). Flap-like limb parts and a restriction of the pleopods to a swimming behavior may represent a retention of "larval" features, and thus provide further evidence for structural and behavioral paedomorphosis with palaeocaridaceans and bathynellaceans being the more derived groups.

HIGHER TAXONOMY AND PHYLOGENY

Problems arise in attempting to assess relationships of taxa within the syncarids. However, these are no more difficult than the problems associated with attempting to assess the position of syncarids in relation to other eumalacostracans. What are the unique characters which define a taxon Syncarida? In the classic scheme of Calman (Fig. 1) Eumalacostraca *sensu stricto* are principally characterized by their caridoid escape reaction (1) and 1-jointed antennal scale (2). The syncarids are a sister group of peracarids and eucarids, defined by a derived feature (3), loss of the carapace (a condition paralleled by a similar loss in the line leading to amphipods and isopods). No opposing shared derived characters, however, join eucarids, with their carapace fused to the thoracomeres (4), and the peracarids, with their oöstegite brood pouch (5).

Schram (1981) and Watling (1981, 1983) have taken up the problems engendered by the Calman system and have offered differing solutions to those difficulties. The Watling model has difficulties in providing shared derived characters at the higher taxonomic levels, and won't be dealt with further here. The system proposed by Schram (1981) had the syncarids as a sister group to the isopods and amphipods. A difficulty with that scheme is that it left no derived features to define the syncarids. A subsequent cladistic analysis (Schram, in press) utilizing 31 characters and a Wagner 78 program,

	4articles in thoracic endopods	5 articles in thoracic endopods
first thoracomere free	Bathynellacea	Palaeocaridacea
first thoracomere fused to cephalon	—	Anaspidacea

FIGURE 2. *Baupläne* one can recognize with the Syncarida. The combination of the first thoracomere fused to the cephalon with 4-segmented thoracopodal endopods was apparently never realized.

while confirming taxa based on *Baupläne* derived from consideration of only 3 characters (Schram 1981), does not second the linking of syncarids with amphipods and isopods. This more recent analysis, however, does generally indicate that Syncarida is a Gilmour-natural taxon, and also reveals that syncarids probably are very primitive animals.

Indeed, several aspects of the biology of living forms would reinforce this conclusion. Although the living anaspidaceans have a caridoid escape reaction, it is imperfectly developed. It typically consists of a single flick of the abdomen that projects the animal up into the water column, after which the animal either passively floats or slowly swims back to the bottom. This is in contrast to the strong caridoid escape reaction seen in the mysidaceans and eucarids. In addition, syncarids lay their eggs free and gastrulate by involution into a blastocoel—both primitive features. However, the development within the egg proceeds to hatching at a rather advanced, free-living stage (early zoeal larval type in bathynellaceans, or miniature version of the adult in anaspids), which are generally considered derived features.

Syncarids are thus generally considered to be a monophyletic taxon. However, discerning possible phylogenetic relationships within the group poses problems. One could recognize 3 basic morphotypes or *Baupläne* (Fig. 2) within the syncarids: a free first thoracomere and less than 5 segments in the thoracopodal endopods (Bathynellacea), a free first thoracomere and 5-segment thoracic endopods (Palaeocaridacea), and a first thoracomere fused to the cephalon and 5 segments in the thoracic endopods (Anaspidacea). The characters used here are the "traditional" ones used for decades to sort major syncarid groups.

Problems arise when one is forced to choose between delineating syncarids primarily on the basis of endopodal segment numbers or on the basis of degree of fusion of the first thoracomere into the cephalon. Different cladograms and classifications of the syncarids also result based on whether palaeocaridaceans are to be perceived as a monophyletic or paraphyletic group.

The traditional approach (Fig. 3) (Brooks 1969, Schminke 1975) essentially discriminates between the bathynellaceans with 4-segmented thoracic endopods (1) and palaeocaridaceans and anaspidaceans which have 5-segmented thoracic endopods. In addition, bathynellaceans have the incisor process of the mandible fused to the tooth row (2), and the eighth thoracopod of males modified for copulation (3). Character (2) is difficult to assess in the palaeocaridaceans, since the mandibles generally are not preserved well enough to be able to evaluate whether they are truly primitive in form (the well-preserved massive mandibles seen in *Palaeocaris,* with its distinct incisor process, may or may not be indicative of all palaeocaridaceans). The palaeocaridacean-

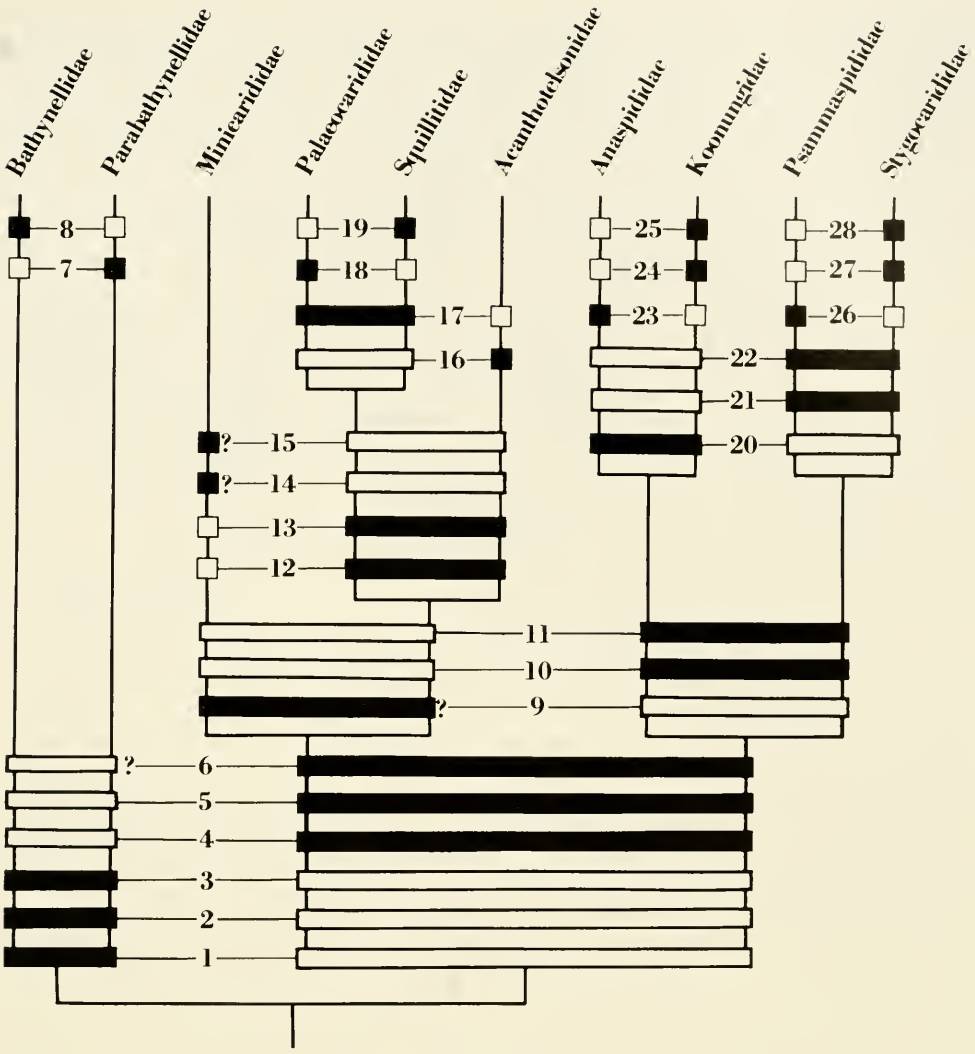


FIGURE 3. A "traditional" presentation of relationships within Syncarida. Derived characters are: 1) 4-segment thoracic endopods, 2) incisor process fused to tooth row, 3) eighth thoracopod copulatory, 4) furcae lacking, 5) first thoracopod typically modified, 6) "precoxae" lacking, 7) paragnaths lacking, 8) diagonal spine row on uropodal protopod, 9) first thoracopod reduced, 10) first thoracomere fused to cephalon, 11) eighth thoracopod not parallel to anterior thoracopods, 12) greatly shortened maxillipedal palp, 13) first thoracomere generally reduced in size, 14) reduction and/or lack of pleopods, 15) pleotelson, 16) anterior thoracopods rapacious, 17) annulate pleopods, 18) massive mandibles, 19) annulate thoracic exopods, 20) large, setose uropod protopod, 21) rostrum separated, 22) maxillule palp lacking, 23) maxillulary palp hook-like, 24) mandibular incisor process lacking, 25) endite lobe on first thoracopod, 26) maxilla proximal endite lacking spine, 27) anus terminal, 28) mandibular palp lacking.

anaspidacean line is delineated by several synapomorphies: lack of caudal furcae (4), a first thoracopod typically modified in some manner (5), and lack of thoracopodal precoxae (6). This last character is difficult to assess, since whether the presence of this feature in some bathynellaceans is really a true precoxal leg joint or just an articulating ring on the body is not clear.

Within the bathynellaceans the Parabathynellidae are characterized by the lack of paragnaths (7), while the Bathynellidae are marked by a uropodal protopod with a diagonal row of spines (8).

The palaeocaridaceans are characterized by a derived feature that is difficult to evaluate. Schminke (1975) was the first to point out that the first thoracopod is apparently reduced in size as well as number of joints in the endopod (9). While this is clearly true for palaeocarids, acanthotelsonids and some squillitids, the form in minicarids is incompletely known. In the latter family the first thoracopod is large, but it is unclear if there is a complete array of 5 segments in the endopod. However, in the squillitid genus *Nectotelson* there is some evidence that indicates the carpus of the first thoracopod is apparently not as large as on thoracopods 2 through 8. Generally, in the former 3 families, besides the greatly shortened maxillipedal palp (12) the first thoracomere is reduced to some degree (13).

Minicaridiidae are very small animals which appear to have a reduced number of pleopods (14). Admittedly this observation could be due to vagaries of preservation; however, the rest of the body and appendages of these creatures are preserved well enough to discern all pertinent features of their structure. The possible presence of a pleotelson among these genera (15) might eventually serve to further define this group.

The Acanthotelsonidae are clearly delineated by the specialized, rapacious form of their anterior thoracopods (16). Within that family, *Uronectes* has only the second thoracic appendages so modified, while *Acanthotelson* and *Palaeosyncaris* have the second and third so specialized. The styloid telson and uropods delineate the species of *Acanthotelson,* whereas a robustly spinescent telson and lateral margin of the uropodal exopod characterize *Palaeosyncaris.*

The palaeocarids and squillitids are characterized by annulate pleopods (17). The Palaeocarididae, though for the most part rather generalized, appear to be distinguished by rather massive mandibles (18). The Squillitidae are unified by their acquisition of annulate thoracic exopods (19). *Squillites* has uniramous pleopods, *Nectotelson* and *Praeanaspides* have biramous pleopods, and *Praenaspides* has a distinctive rectangular and laterally spinose telson.

Schminke (1975) has clearly analyzed the distribution of characters within the Anaspidacea, and these are repeated here only for completeness. Anaspidaceans are united in possessing a first thoracomere completely fused to the cephalon (10) and the eighth thoracopod offset at an angle and not parallel to the other thoracopods (11). The anaspids and koonungids have a large and setose uropodal protopod (20), while psammaspids and stygocarids have a separated rostrum (21) and lack a palp on the maxillules (22). Anaspididae are distinguished by having the maxillulary palp reduced to a hook-like spine (23), and the Koonungidae lack an incisor process on the mandible (24) and have an endite lobe on the first thoracopod (25). The Psammaspididae have no spine on the proximal endite of the maxillae (26), while the Stygocarididae have a terminal anus (27) and lack a mandibular palp (28).

A classification of Syncarida produced from the above analysis is similar to that usually encountered for the group, except that a more natural array of palaeocaridacean families is established than that used by Brooks (1962*a, b,* 1969).

Order Syncarida Packard, 1885
- Suborder Bathynellacea Chappuis, 1915
  - Family Bathynellidae Chappuis, 1915
  - Family Parabathynellidae Noodt, 1965
- Suborder Palaeocaridacea Brooks, 1962
  - Family Minicaridiidae, nov.
  - Family Palaeocarididae Meek & Worthen, 1865
  - Family Squillitidae Schram & Schram, 1974
  - Family Acanthotelsonidae Meek & Worthen, 1865
- Suborder Anaspidacea Calman, 1904
  - Family Anaspididae Thompson, 1894
  - Family Koonungidae Sayce, 1908
  - Family Psammaspididae Schminke, 1974
  - Family Stygocarididae Noodt, 1963

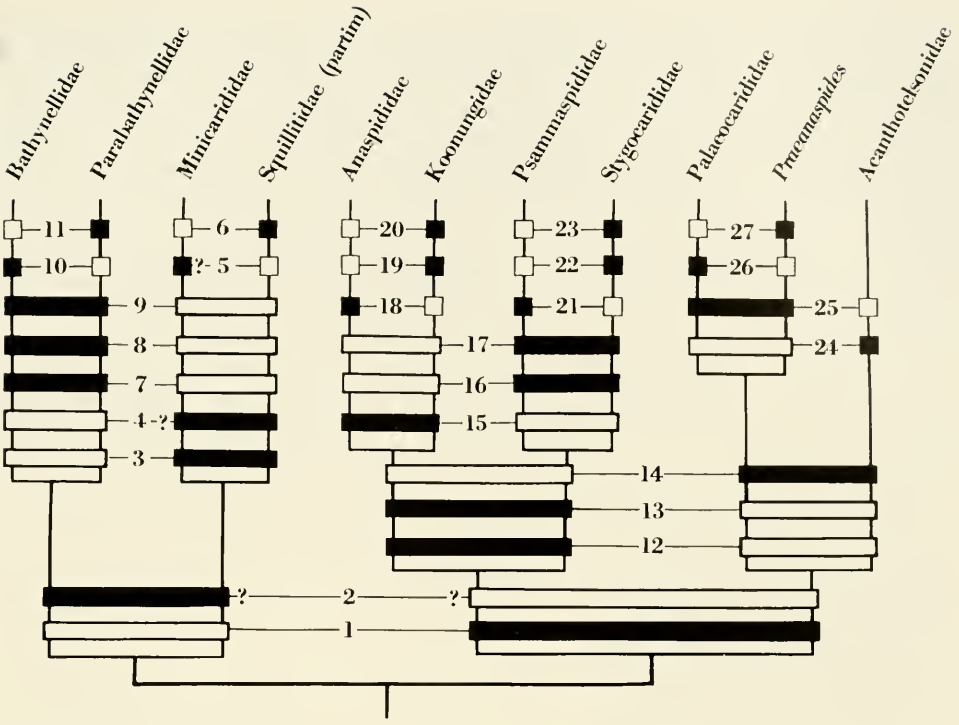


FIGURE 4. An alternative presentation of relationships within Syncarida. Derived characters are: 1) first thoracomere reduced or fused to cephalon, 2) incisor process fused to tooth row, 3) furcae lacking, 4) first thoracopod modified, 5) reduced and/or absent pleopods, 6) annulate thoracic exopods and pleopods, 7) 4-segmented thoracic endopods, 8) reduced and/or absent pleopods, 9) eighth thoracopod copulatory, 10) diagonal spine row on uropodal protopod, 11) paragnaths lacking, 12) first thoracomere fused to cephalon, 13) eighth thoracopod not parallel to anterior thoracopods, 14) greatly reduced maxillipedal palp, 15) large, setose uropodal protopod, 16) rostrum separate, 17) maxillulary palp lacking, 18) maxillulary palp hook-like, 19) mandibular incisor process lacking, 20) endite lobe on first thoracopod, 21) maxilla proximal endite lacking spines, 22) anus terminal, 23) mandibular palp lacking, 24) anterior thoracopods rapacious, 25) annulate pleopods, 26) massive mandibles, 27) annulate thoracic exopods.

An alternative analysis of cladistic relationships (Fig. 4) can be performed for syncarids with initial assumptions somewhat different from those of the traditional system presented above. Rather than make the first dichotomy one based essentially on numbers of segments in thoracic endopods, one could distinguish between syncarids with no modification of the first thoracomere and those with a first thoracomere modified in some way (1). The former line includes the bathynellaceans and might be further characterized by mandibles (2) with an incisor process fused to the tooth row (as noted above, a character impossible to verify as yet on all the fossils). This line divides into a branch leading to some fossil families which lack furcae (3) and which may have a first thoracopod modified from the form seen in the second through eighth thoracopods (4). Within this branch, the Minicaridadae apparently lack or have a reduced number of pleopods (5) while the Squillitidae (in part, including *Nectotelson* and *Squillites*) have annulate thoracic exopods and pleopods (6).

The branch leading to the bathynellaceans of course delineates the 2 families on the basis of the bathynellid's possession of a diagonal row of spines on the uropodal protopod (10) and by the parabathynellid's lack of a paragnath (11).

The Anaspidacea fuse the first thoracomere into the cephalon (12) and have the eighth thoracopod offset from the seventh thoracopod (13). The opposing branch with its reduced but free thoracomere and parallel seventh and eighth thoracopods possess

a derived reduction in the first thoracopodal endopod being very short (14). The anaspid/koonungid line, as above, have large and setose uropodal protopods (15); and within that the Anaspididae have a hook-like maxillulary palp (18), while Koonungidae lack a mandibular incisor process (19) and have gnathobasic lobes on the first thoracopod (20). The psammaspid/stygocarid line has a separate rostrum (16) and lacks a maxillulary palp (17). The Psammaspididae lack spines on the proximal endites of the maxillae (21), while the Stygocaridiidae have a terminal anus (22) and lack a mandibular palp (23).

The Acanthotelsonidae have rapacious anterior thoracopods (24), while the palaeocarid/squillitid group has annulate pleopods (25). The Palaeocaridiidae have massive mandibles (26), and *Praeanaspides* (a squillitid) has annulate thoracic exopods (27).

This analysis could yield a classification somewhat different than the traditional, in that essentially 4 groups can be recognized. Brooks' order Palaeocaridacea emerges as a polyphyletic taxon, thus the major groups might best be recognized as superfamilies.

Order Syncarida
- Superfamily Bathynelloidea
  - Family Bathynellidae
  - Family Parabathynellidae
- Superfamily Minicaridoidea
  - Family Minicaridiidae
  - Family Squillitidae (in part)
- Superfamily Palaeocaridoidea
  - Family Palaeocaridiidae
  - Family Acanthotelsonidae
  - ? *Praeanaspides*
- Superfamily Anaspidoidea
  - Family Anaspididae
  - Family Koonungidae
  - Family Psammaspidae
  - Family Stygocaridiidae

In many respects, this second arrangement is an unsatisfactory system. The differences encapsulated in these 2 classifications of the syncarids arises from a dichotomy involved in outgroup comparison of the "palaeocaridaceans," and in both schemes it involves establishing derived characters in the Paleozoic families. The problem could be expressed as a simple dilemma derived from initial consideration of the syncarid morphotypes: which is more important, the fusion of first thoracomere into the cephalon, or the loss of a joint in the thoracopodal endopods? The initial "weighting" determines the course of the subsequent analysis.

In the traditional scheme (Fig. 3) 28 apomorphies are used to define the 10 families of Syncarida; in the alternative scheme (Fig. 4) there are 27 apomorphies to separate 11 "family" level taxa. The traditional scheme thus seems to possess slightly more information value. It also more clearly justifies its initial dichotomy (based on joint number in thoracic endopods) with the greatest number of congruent features. For these last reasons, as well as the fact that the alternative scheme requires too many uncertain judgments at this time involving the poorly known minicaridoids, I have opted in the systematic section of this monograph to retain the traditional classification of syncarids into suborders. However, more detailed and exacting knowledge of the minicarids and *Nectotelson* someday may allow a more reasoned selection to be made between these two systems.

Nevertheless, the problem of analyzing syncarid phylogeny is not so easily disposed of (as if the above taxonomic dilemma were easy). Both of the schemes above take for granted essentially the same position in regard to polarity of a basic character in the group, viz, that the primitive condition is one in which the first thoracomere is free

and large, and that increasing specialization is achieved as this segment is reduced and eventually fused into the cephalon. Is this necessarily the case?

Schminke (1981) presents a well-documented series of arguments for the progenetic paedomorphic derivation of bathynellaceans from some ancestral syncarid condition in which an adult animal, presumably of a palaeocarid or anaspid form, had a long larval sequence. If we extend Schminke's arguments, might we not question whether the anatomical stages seen in bathynellaceans (large and free first thoracomere, flap-like thoracic exopods, reduced number of thoracic endopodal segments, reduced or missing pleopods, and caudal furcae) are really primitive? Rather, might we not consider these features to be actually derived by the agency of progenesis from some ancestral adult in which none of these "larval" features were expressed. In such an interpretation, the most "primitive" adult state would be one in which the first thoracomere is fused to the cephalon, and that the manifestations of successive degrees of freedom of the first thoracomere are increasingly derived.

This assumption involving a reversed polarity would lead in turn to a rather controversial cladistic analysis (Fig. 5). A bathynellacean/palaeocaridacean line would be characterized by the presence of a free first thoracomere (1), the anaspidacean line by the eighth thoracopod being offset from and not parallel to the seventh (2).

The characterizations within the Anaspidacea follow those already given above: large, setose uropodal protopods in anaspids and koonungids (3), a separate rostrum (4) and no maxillulary palp (5) in psammaspids and stygocarids, a hook-like palp on the maxillule (6) in anaspids, lack of a mandibular incisor process (7) and endite lobes on the first thoracomere (8) in koonungids, lack of spines on the proximal endite of the maxilla (9) in psammaspids, and a terminal anus (10) and lack of a mandibular palp (11) in the stygocarids.

The Bathynellacea share several advanced characters: a 4-segment thoracic endopod (12), fusion of the incisor process to the tooth row in the mandible (13), a copulatory eighth thoracopod in the male (14), and a first thoracomere as large as any succeeding thoracomere (15). The Palaeocaridacea lack furcae (16).

The bathynellids have a diagonal row of spines on the uropodal protopod (17), while the parabathynellids lack paragnaths (18).

Within the palaeocaridaceans, the minicarid/squillitid (in part) line convergently develops the enlarged first thoracomere (19), while the other families have a reduced endopod on the first thoracopod (20). The minicarids apparently have reduced or absent pleopods (21), while the squillitids have annulate thoracic exopods and annulate pleopods. The acanthotelsonids have rapacious anterior thoracopods (23), while the palaeocarid/*Praeanaspides* line has annulate pleopods (24). The palaeocarids have massive mandibles (25) and the *Praeanaspides* also possess annulate thoracic exopods (26).

The above scheme in comparision with the traditional and alternative schemes discussed earlier unfortunately uses only 26 apomorphies to define its end points and has a rather high number of convergent characters. Note, however, that the taxonomy which results from this cladogram is similar to that of the traditional classification, except that the Anaspidacea in this latter scheme are felt to be closest to the primitive condition, and the Squillitidae *sensu stricto* are separated from the genus *Praeanaspides*.

Still another analysis alternative to the above is possible (Fig. 6) also involving the reversed polarity, but utilizing only 25 apomorphies. The anaspidoid line is as above. The bathynelloid/minicaridoid line has an enlarged first thoracomere (12), while the palaeocaridoid line has a reduced endopod on the first thoracopod. The bathynelloid line has the 4-segment endopod (14), incisor process fusion (15), and copulatory eighth thoracopod (16) noted before; and the minicaridoid line has a problematic apomorphy difficult to assess because of preservation, i.e., the first thoracopod large but possibly not structurally identical to the second and following thoracopods (17). The family apomorphies [Bathynellidae (18), Parabathynellidae (19), Minicaridiae (20), Squillitidae (in part) (21), Acanthotelsonidae (22), Palaeocarididae (23, 24), and *Praeanaspides* (23, 25)] are all those noted in the schemes already discussed, especially that in Figure 5.

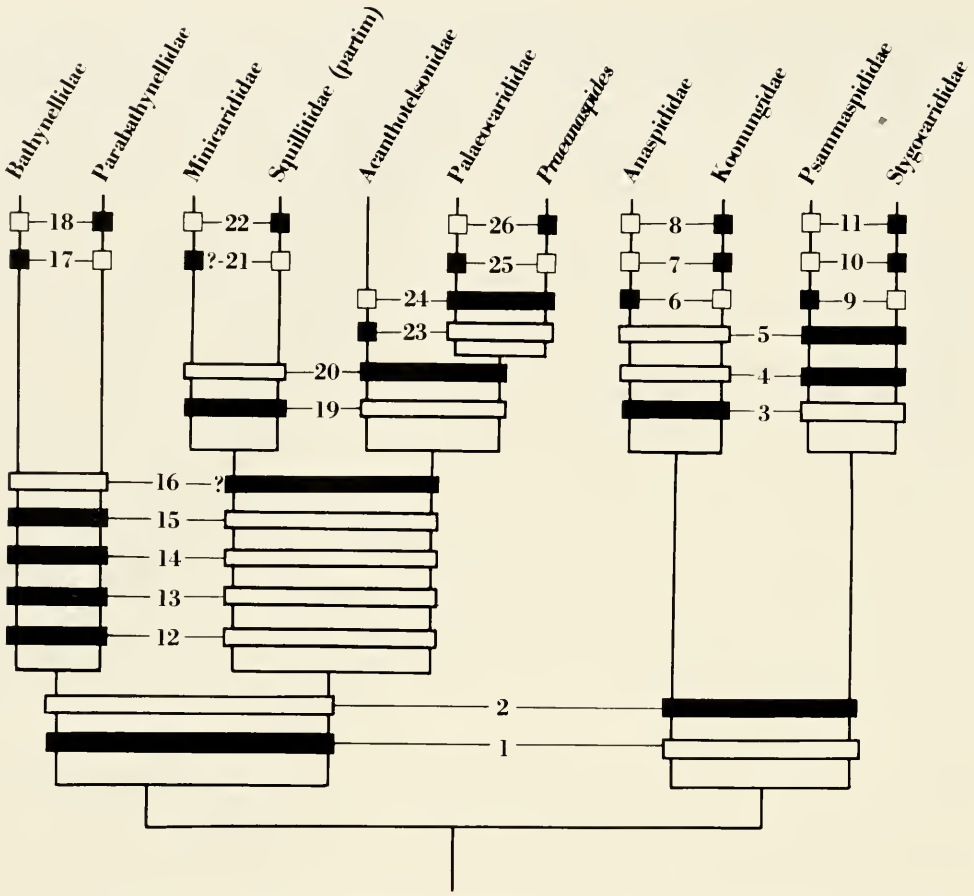


FIGURE 5. Relationships within Syncarida involving reversed polarity with loss of fusion of the first thoracomere with the cephalon due to paedomorphosis. Derived characters are: 1) first thoracomere free, 2) eighth thoracomere not parallel to anterior thoracopods, 3) large, setose uropodal protopod, 4) rostrum separate, 5) maxillulary palp lacking, 6) maxillulary palp hook-like, 7) mandibular incisor process lacking, 8) endite lobe on first thoracomere, 9) maxillary proximal endite lacking spines, 10) anus terminal, 11) mandibular palp lacking, 12) 4-segment thoracic endopod, 13) incisor process fused to tooth row, 14) eighth thoracopod copulatory, 15) first thoracomere subequal to any succeeding thoracomeres, 16) furcae lacking, 17) diagonal spine row on uropod protopod, 18) paragnaths lacking, 19) first thoracomere subequal to any succeeding thoracomeres, 20) greatly reduced maxillipedal palp, 21) reduced and/or absent pleopods, 22) annulate thoracic exopods and pleopods, 23) anterior thoracopods rapacious, 24) annulate pleopods, 25) massive mandibles, 26) annulate thoracic exopods.

This last cladogram corresponds to the alternative classification given above, except that the superfamily Anaspidoidea is now presented as the closest to a primitive condition for Syncarida as a whole.

What can we conclude about syncarid evolution? We should be cognizant of some level of uncertainty as to just how these taxa are related to each other. However, a more definitive resolution of the problem must await better and more detailed information about the Paleozoic syncarids. Characters which delineate the living and fossil families are not equivalent in the sense that the living families are separated on the basis of details of mouthparts, whereas the fossil families are largely resolved on the basis of gross form of trunk appendages. Ideally, more mouthpart data for Palaeocarideacea could have allowed a more complete data matrix than that used here to be analyzed with a Wagner 78 program. The resultant rigor could have mathematically determined parsimony and homoplasy. However, phylogenetic trees and taxonomies are pragmatic instruments (Charig 1982, Schram 1983), and the lack of any data that we would like to have should not be an excuse for not attempting to organize that

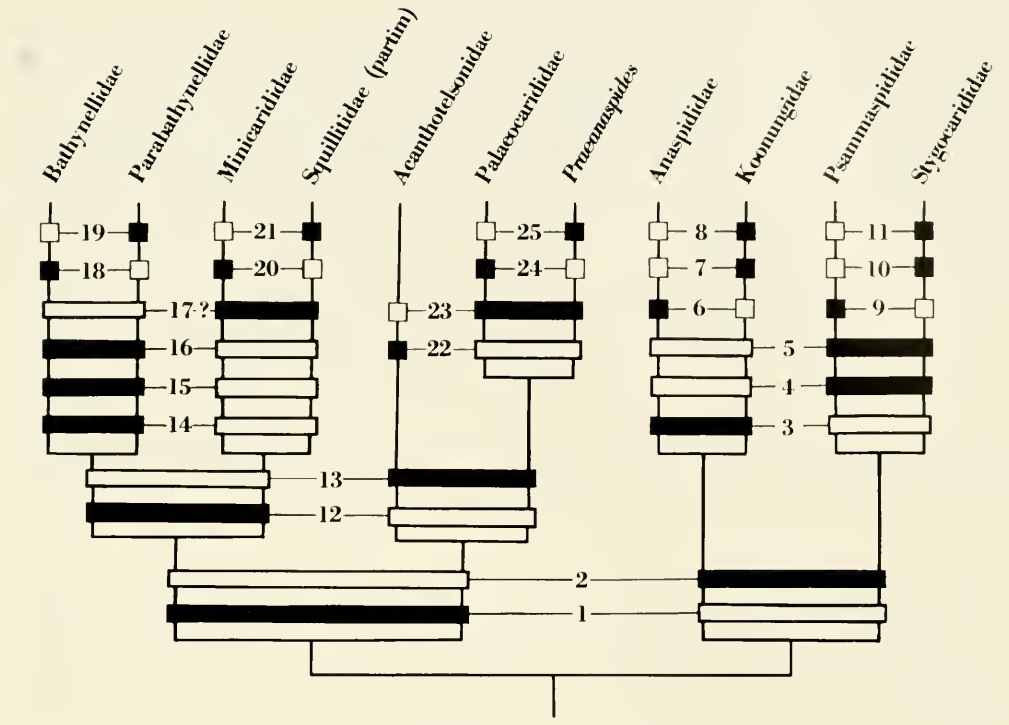


FIGURE 6. An alternative presentation of relationships within Syncarida involving reversed polarity with loss of fusion of the first thoracomere with the cephalon due to paedomorphosis. Derived characters are: 1) first thoracomere free, 2) eighth thoracomere not parallel to anterior thoracopods, 3) large, setose uropodal protopod, 4) rostrum separate, 5) maxillulary palp lacking, 6) maxillulary palp hook-like, 7) mandibular incisor process lacking, 8) endite lobe on first thoracomere, 9) maxillary proximal endite lacking spines, 10) anus terminal, 11) mandibular palp lacking, 12) first thoracomere, 13) reduced endopod on first thoracopod, 14) 4-segment thoracic endopod, 15) incisor process fused to tooth row, 16) eighth thoracopod copulatory, 17) ? form of first thoracopod, 18) diagonal spine row on uropod protopod, 19) paragnaths lacking, 20) reduced and/or absent pleopods, 21) annulate thoracic exopods and pleopods, 22) anterior thoracopods rapacious, 23) annulate pleopods, 24) massive mandibles, 25) annulate thoracic exopods.

information which we do have. We should simply recognize the limits of the information at hand, and be aware of its effect on the level of uncertainty engendered in our present understanding of syncarid evolution. Nevertheless, I would hope that the organization of the fossil Syncarida used here is more adequate than anything that we have had heretofore.

SYSTEMATICS

The system of annotated synonymy, summarized by Matthews (1973), is used in this section of the monograph. This should facilitate use and evaluation of my systematic decisions by any future workers.

Order SYNCARIDA Packard, 1885
Suborder PALAEOCARIDACEA Brooks, 1962
Family MINICARIDIDAE nov.

Diagnosis.—Thoracic exopods unisegmental. Pleopods unisegmental, if present. First thoracomere large, not reduced nor fused to cephalon.

Type genus.—*Minicaris* Schram, 1979.

Remarks.—The distinctive nature of the first thoracomere and the unisegmental or flap-like form of the pleopods when present clearly warrants separate family status.

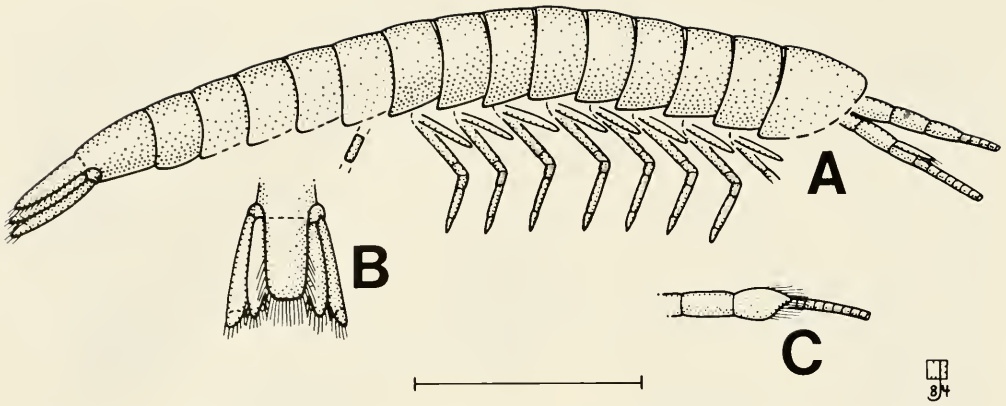


FIGURE 7. A) Reconstruction of *Minicaris brandi*, scale 2 mm (redrawn from Schram 1979*a*); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

In addition, the small size, possible absence of posterior pleopods, the possible presence of a pleotelson, and the early age (Lower Carboniferous) is of interest with regard to a parallelism to, or a possible origin of, the Bathynellacea (*see* Higher Taxonomy and Phylogeny section).

Genus MINICARIS Schram, 1979*a*

Diagnosis.—Peduncles of antennules and antennae subequal. At least first pleopod present and well developed. Uropods narrow and blade-like. (?)Pleotelson.

Type species.—*Minicaris brandi* Schram, 1979*a*.

Minicaris brandi Schram, 1979*a*
Fig. 7

v.*1979*a Minicaris brandi* Schram, p. 109, figs. 52 & 53.
1979b Minicaris brandi Schram. Schram, p. 170, table 2.
1981 Minicaris brandi Schram. Schram, p. 131, table 2, fig. 6D.
1982 Minicaris brandi Schram. Wood, p. 577.
1982 Minicaris brandi Schram. Schram, p. 122, fig. 8A.

Diagnosis.—Since there is but one species, the diagnosis is the same as that of the genus.

Holotype.—GSE 13056. Long Livingston Borehole no. 25, West Lothian, Scotland. 1071–1151 foot section, below Pumpherstone Shell Bed, Lower Oil Shale Group, Dinantian, Lower Carboniferous.

Other locality.—Questionably reported from along Manse Burn, Bearsden, near Glasgow, Scotland, in shales equivalent to the Top Hosie Limestone, lowermost Namurian (Wood 1982).

Description.—Antennular peduncle 3 joints, proximal-most joint one-half total length of peduncle, distal 2 joints progressively shorter. Antennal protopod distal joint twice the proximal, scaphocerite oval with distal tip pointed and setose, proximal 2 flagellar joints peduncular. Thoracomeres with rounded pleura, posterior corners acute. Thoracopodal exopods narrow. All thoracopods appear equal, ischium long, merus and carpus short, propodus moderate, dactylus short. Abdominal pleura rounded. If not a true pleotelson, telson not sharply sutured from sixth pleomere. Telson spade-like, setose. Uropods blade-like, setose, possibly with diaeresis.

Remarks.—Reexamination in 1980 of the holotype, and still only good specimen of this species, confirmed all the pertinent points of the anatomy above. The lack of

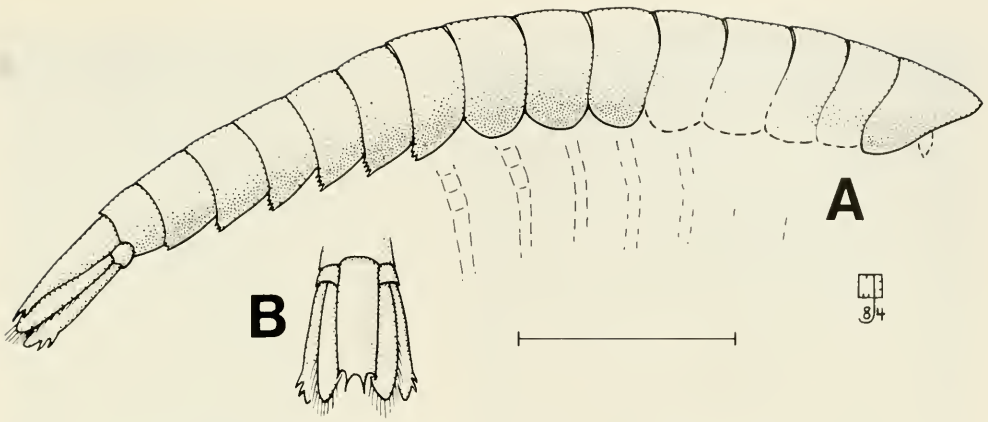


FIGURE 8. A) Reconstruction of *Erythrogaulos carrizoensis*, scale 2 mm; B) tailfan to same scale as body.

all but the first pleopod in the abdominal series is still not completely understood. It is possible the more posterior pleopods were not preserved, but it is also possible that they were never there to begin with. The small size (8 mm) and general form of the animal might indicate a possibility of paedomorphosis in the evolution of this taxon, since so many of the living small syncarids do not develop complete series of pleopods nor completely separate the telson from the last pleomere. Only more and better material can allow us to choose between these alternatives.

Genus ERYTHROGAULOS new genus

Diagnosis.—Posterior corners of pleomere pleura serrate. Telson distally spinose. Uropodal exopod distally spinose.

Type species.—*Erythrogaulos carrizoensis* new species.

Etymology.—A reference to the stratigraphic horizon, Red Tanks Member, Madera Formation, Lower Permian.

Erythrogaulos carrizoensis new species
Fig. 8; Plate 1, figs. A & B

Diagnosis.—Since there is but one species, the diagnosis is the same as that of the genus.

Holotype.—SDSNH 25141 (Plate 1, figs. A & B). Carrizo Arroyo, Lucero Mts., southeastern Valencia County, New Mexico. Upper Red Tanks Member, Madera Formation, Wolfcampian, Lower Permian. (Collected by Dr. Jarmilla Kukalova-Peck, Carlton University, Ottawa, Ontario, Canada.)

Etymology.—After the type locality in Carrizo Arroyo.

Description.—Body small. Thoracomeres subequal, pleura apparently rounded, except eighth which appears posteriorly serrate. Pleomeres subequal, posterior corners of at least first 3 pleura serrate. Telson rectangular, developed distally with 2 sets of tooth-like spines, medial distal set larger than lateral proximal pair. Uropodal rami, blade-like and subequal, slightly longer than telson, exopod with distal tooth-like spines on lateral margin just anterior of where diaeresis might be, endopod margins finely setose.

Remarks.—Only one specimen allows any inference to be made concerning the anatomy of the animal. Two other specimens (SDSNH 29140) appear to preserve only part of the trunk segment series. The observed thoracopods are of such a diaphanous preservation as to preclude any more concrete conclusions about them other than that they seem to be equally developed back to and including the eighth pair. None of the

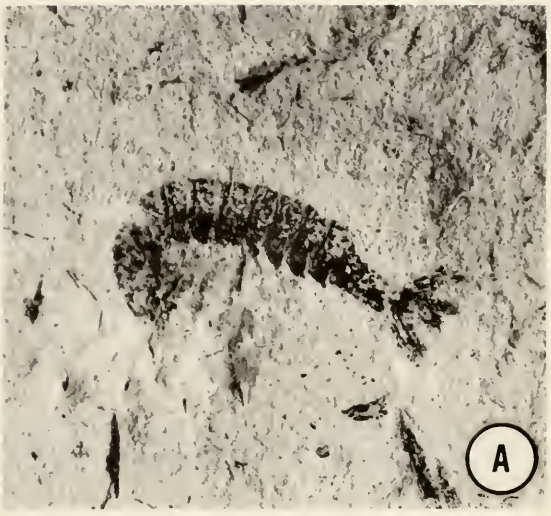


PLATE 1

FIGURES A & B. *Erythrogaulos carrizoensis* new species, holotype, SDSNH 25141; A) whole specimen, ×7; B) closeup of posterior abdomen and tailfan, note spines on posterior of pleura (p), spines on distal telson (t) and lateral margin of uropodal exopod (e), and setose margins of uropodal rami (arrows), ×19.6.

FIGURES C–E. *Acanthotelson stimpsoni* Meek and Worthen, 1865; C & D) latex peels of holotype, X 346, ×1.7; E) syntype of *A. eveni* Meek and Worthen, 1868, ISGS 3066 (made a junior synonym of *A. stimpsoni*, by Packard 1886), ×1.2.

anterior limbs seemed specialized in any way, though these had to be partly destroyed in preparation in order to fully reveal the cephalon. No traces of pleopods were noted, and this, combined with the fact that thoracopods are clearly detectable and with the general small size of the body, might suggest the possibility, as with *Minicaris brandi*, that pleopods were either greatly reduced or not present on this species.

The distinctively serrate pleura and spinose telson warrant separate generic status for this species from its nearest relative, *Minicaris brandi* of the Lower Carboniferous.

The associated biota in the Red Tanks Member includes: numerous plants dominated by the gymnosperm genera *Walchia* and *Cordaites*, but also including *Callipteris*, sphenopsids, and lycopsids; a most diverse array of uniramians including insects and myriapods; the eurypterid *Adelophthalmus luceroensis*; ostracodes; brachiopods; and spirorbid worms. Kues and Kietzke (1981) interpret the paleoecology of the Carrizo Arroyo fauna as representing a fresh to brackish water habitat on a delta plain. The extreme delicacy of the preservation from this locality also indicates quick burial under anoxic conditions with little postdepositional disturbance.

Family ACANTHOTELSONIDAE Meek and Worthen, 1865

Diagnosis.—Thoracic exopods unisegmental and flap-like. Anterior thoracopods raptorial. Pleopods biramous and flap-like.

Type genus.—*Acanthotelson* Meek & Worthen, 1865.

Remarks.—Brooks (1962*a*, *b*) chose to place the genera *Acanthotelson* and *Uronectes* in separate families based on the degree of raptorial development expressed in the anterior thoracopods. Although this is an important character, it is best utilized for distinction at the generic level. The unisegmental, flap-like nature of the thoracic exopods and rami of the pleopods in comparison to other palaeocaridacean families herein recognized warrants uniting all species with raptorial thoracopods into a single family.

Genus ACANTHOTELSON Meek and Worthen, 1865

Diagnosis.—First thoracopod markedly reduced. Second and third thoracopods raptorial. Telson and uropods styliform.

Type species.—*Acanthotelson stimpsoni* Meek and Worthen, 1865.

Acanthotelson stimpsoni Meek and Worthen, 1865
Fig. 9; Plate 1, figs. C–E, Plate 2, fig. A

v.*1865 *Acanthotelson stimpsoni* Meek and Worthen, p. 47.
v. 1866 *Acanthotelson stimpsoni* Meek and Worthen. Meek and Worthen, p. 401, pl. 32, figs. 6, 6a–f.
1868a Acanthotelson eveni Meek and Worthen. Meek and Worthen, p. 27.
v. 1868*b Acanthotelson stimpsoni* Meek and Worthen. Meek and Worthen, p. 549, 2 figs.
v. 1868*b Acanthotelson eveni* Meek and Worthen. Meek and Worthen, p. 551, 4 figs.
1880 *Acanthotelson stimpsoni* Meek and Worthen. Brocchi, p. 10, pl. 1, fig. 11.
1884 *Acanthotelson stimpsoni* Meek and Worthen. White, p. 176, pl. 37, fig. 4–5.
1184 *Acanthotelson eveni* Meek and Worthen. White, p. 177, pl. 38, figs. 4–7.
v. 1886*a Acanthotelson stimpsoni* Meek and Worthen. Packard, p. 123, pl. 1, figs. 1–3, pl. 2, figs. 1–3.
1886*a Acanthotelson eveni* Meek and Worthen. Packard, p. 125.
1890 *Eileticus anthracinus* Scudder, p. 420, pl. 38, fig. 5.
1890 *Eilecticus aequalis* Scudder, p. 421, pl. 38, figs. 6–9.
1896 *Acanthotelson stimpsoni* Meek and Worthen. Calman, p. 799, pl. 2, fig. 16.
1901 Acanthotelson species Fritsch, p. 74, fig. 398.
1909 Acanthotelson stimpsoni Meek and Worthen. Smith, p. 575, fig. 62.
1911a Acanthotelson stimpsoni Meek and Worthen. Calman, p. 159.
1911a Acanthotelson eveni Meek and Worthen, Calman, p. 159.
1916 Acanthotelson stimpsoni Meek and Worthen. Cockerell, p. 234.
1916 Acanthotelson stimpsoni Meek and Worthen. Vanhöffen, p. 146, fig. 12.
1916 Acanthotelson eveni Meek and Worthen. Vanhöffen, p. 148.
1916 Acanthotelson species. Vanhöffen, p. 148, fig. 14.
1919 Acanthotelson species. Pruvost, p. 85.
1927 Acanthotelson stimpsoni Meek and Worthen. Chappuis, p. 605.

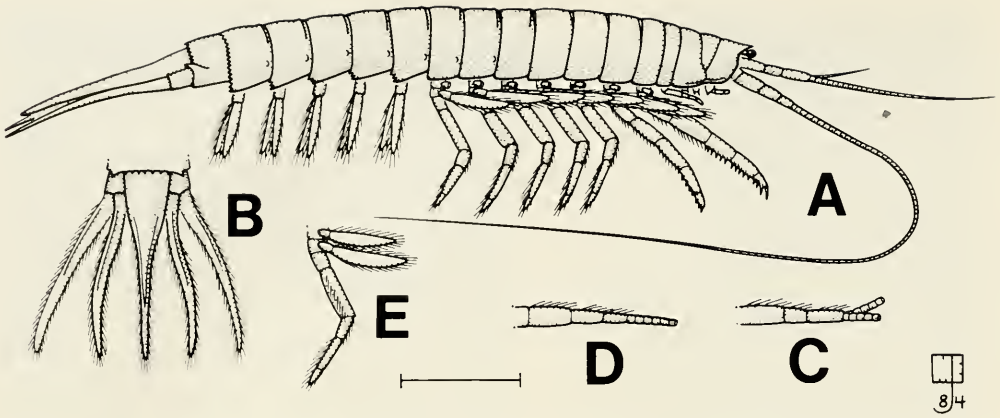


FIGURE 9. A) Reconstruction of *Acanthotelson stimpsoni,* scale 5 mm (modified from Brooks 1962*b*); B) tailfan to same scale as body; dorsal views of C) right antennule and D) antenna; E) posterior thoracopod. Appendages slightly enlarged.

1931 Acanthotelson eveni Meek and Worthen. Van Straelen, p. 11.
1931 Acanthotelson stimpsoni Meek and Worthen. Van Straelen, p. 12.
1959 Acanthotelson eveni Meek and Worthen. Siewing, p. 2.
1959 Acanthotelson stimpsoni Meek and Worthen. Siewing, p. 3.
1962*a Acanthotelson stimpsoni* Meek and Worthen. Brooks, p. 236.
v. 1962*b Acanthotelson stimpsoni* Meek and Worthen. Brooks, p. 230, pls. 55–59; Text-pl. 10, 11a.
1965 Acanthotelson species Noodt, p. 83.
1969 *Acanthotelson stimpsoni* Meek and Worthen. Brooks, p. R355, figs. 165-2, 171.
1969a Acanthotelson stimpsoni Meek and Worthen. Schram, p. 219, Table 1.
1969b Acanthotelson stimpsoni Meek and Worthen. Schram, p. 201.
1976a Acanthotelson stimpsoni Meek and Worthen. Schram, p. 21.
1976b Acanthotelson stimpsoni Meek and Worthen. Schram, p. 411.
1979a Acanthotelson stimpsoni Meek & Worthen. Schram, p. 28, Table 1.
1979b Acanthotelson stimpsoni Meek and Worthen. Schram, p. 167, fig. 1, Table 2.
1981a Acanthotelson stimpsoni Meek and Worthen. Schram, p. 131, text-fig. 5b, Table 2.
1981b Acanthotelson stimpsoni Meek and Worthen. Schram, p. 9, fig. in text.
1982 Acanthotelson eveni Meek and Worthen. Kent, p. 15.

Diagnosis.—Second joint of antennal peduncle shorter than first or third. Telson styliform, equal to or slightly longer than uropods.

Lectotype.—X 346 (Plate 1, figs. C and D). Mazon Creek area, Will County, Illinois. Francis Creek Shale, Carbondale Formation (Westphalian C), Pennsylvanian. (Improperly designated a holotype by Brooks 1962*b*.)

Other localities.—(See Schram 1976*a*) Illinois State Geol. Surv. core T-4 (816 feet) NW ¼, SW ¼, SE ¼, sec 25, T2S, R14W, Wabash County Illinois; Dykersburg Shale, Carbondale Formation, Pennsylvanian. Sec. 4, T9S, R1E, ½ mile west of Carterville, Williamson County; gray shale above #6 (Herrin) Coal, Brereton Cyclothem, Pennsylvanian. Abandoned Chieftan Mine, 7 miles south of Terre Haute, Indiana, east of Highway 41; Lower Shelburn Formation, Pennsylvanian.

Description.—Cephalon with short rostrum, cervical and precervical grooves. Eyes small and stalked. Antennular peduncle 3-segmented, proximal and distal joints large, medial segment short, flagella well developed with inner branch shorter than outer branch. Antennal protopod with short proximal segment bearing nephropore and long distal segment, no scaphocerite, very long flagellum with proximal 2 joints peduncular. Antennules and antennae with setose inner peduncular margins. Mandible massive, palp well developed. Maxillule with 3-segment palp. Maxilla with at least proximal segment of palp large.

First thoracomere reduced in length. Second through fourth thoracomeres progressively longer than first. Last 4 thoracomeres subequal, last 3 thoracomeres have

anterior margins with raised ridge. Thoracic pleura simple. First thoracopod reduced, possibly as short maxillipede. Second and third thoracopods biramous, endopods large, spinose, and raptorial in form. Five posterior thoracopods of ambulatory form, with epipodites, exopods of single segment (flap-like), endopods with short ischium and dactylus, and long merus, carpus, and propodus joints.

Pleomeres similar in size to posterior thoracomeres, first through fifth pleura with posterio-ventral corners serrate, fifth and sixth pleomere posterior margins serrate. Sixth pleomere not elongate. Pleopods as biramous setose paddles. Telson as long spike, margins with alternating spines and setae. Uropodal rami as blades, margins with alternating spines and setae. Spikes or uropods and telson reinforced with median ridges.

Remarks.—Though recognized as a distinct taxon since the time of Meek and Worthen (1865); a complete and reliable description and accurate reconstruction of *A. stimpsoni* was not available until Brooks (1962*b*). However, actual photo illustrations of the type series of *A. stimpsoni* have not been prepared until now, except for the single exception of Brooks (1962*b*, pl. 54, fig. 4). Latex peels illustrated here of the lectotype, X346 (Plate 1, figs. C and D), are taken from the specimen which was used as the basis for one of the drawings in Meek and Worthen (1868*b*:549, fig. B). A paralectotype, X3442, (Plate 2, fig. A) was the basis for another drawing in Meek and Worthen (1868*b*:549, fig. A). The tail on X3442 was also apparently used by Meek and Worthen as an addition to augment their drawing (p. 551, fig. A) of ISGS 3066 (Plate 1, fig. E). ISGS 3066 is also a syntype of another species, *A. eveni,* since synonymized (Packard 1886) with *A. stimpsoni.*

Heretofore, understanding of what constitutes the genus *Acanthotelson* has been clouded incredibly by the incorrect use of the name *Eileticus* Scudder, 1882, by European workers. *Eileticus* (*sensu stricto*) is now generally conceded to be a myriapod. However, as pointed out by Brooks (1962*b*:258), Scudder designated as a separate taxon, *E. aequalis,* what turned out to be a poorly preserved specimen of *A. stimpsoni.* Some European workers built upon this confusion and have applied the name *Eileticus* to other taxa that have turned out not to be *Acanthotelson.* For example, *E.* cf. *aequalis* of Pruvost (1919) is probably *Pleurocaris,* and *E. pruvosti* Vandenberghe (1960) is likely better placed in *Nectotelson.* Each of these cases is discussed in detail elsewhere, under the appropriate taxon designation.

Acanthotelson kentuckiensis new species

by
Frederick R. Schram and Donald Chesnut*
*Kentucky Geological Survey, Lexington

Fig. 10; Plate 2, figs. B–F

Diagnosis.—Segments of antennular peduncles subequal. Telson subtriangular but long and narrow, shorter than uropods.

Holotype.—SDSNH 23722 (Plate 2, fig. B). Black Oak Coal, Inc. strip mine, near Silverville, McCreary County, Kentucky, 2 miles north of Tennessee state line; 84°26′30″ N, 36°38′42″ W. Black fissile shale above River Gem Rider Coal, Lower Breathitt Formation, Middle Pennsylvanian.

Other material.—SDSNH 23723 (Plate 2, fig. E), 23724, 23725.

Descriptions.—Antennules well developed, with 3 subequal segments (Plate 2, fig. F) composing the peduncle, about equal in size to peduncle of antennae. Antennal peduncular segments apparently short, no scaphocerite noted.

All pleomeres about equal in length, last 3 with paired longitudinal dorsal ridges, dorsal posterior margin of sixth pleomere concave. Telson (Plate 2, figs. C & D) triangular in outline, narrow, with dorsal median ridge, margins furrowed and setose, distal setae more strongly developed. Uropodal rami styliform, each with reinforcing rib flanked by slight furrows, exopodal margins with strong setae (especially laterally), endopodal margins finely setose.

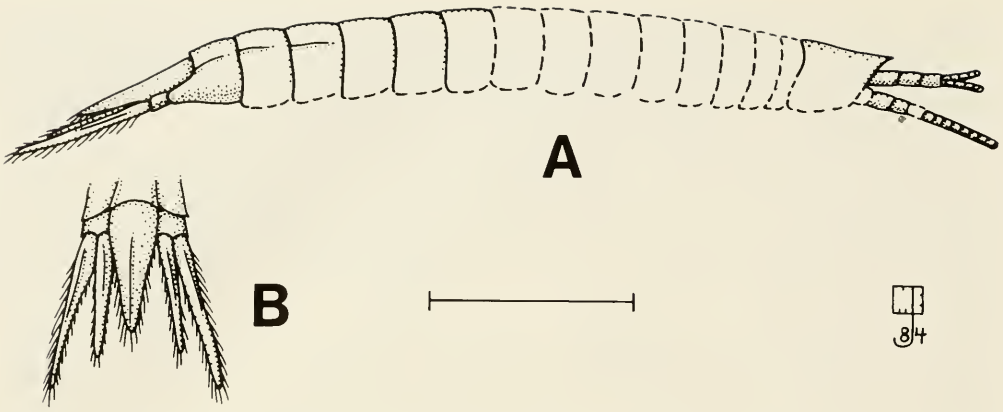


FIGURE 10. A) Diagrammatic rendition of what is currently known about the form of *Acanthotelson kentuckiensis,* scale 5 mm; B) tailfan to same scale as body.

Remarks.—The most complete specimen (SDSNH 23722) lacks a thorax and all other specimens are of tailfans only. However, though anatomical information about this species is minimal, the distinctive nature of the tailfan, especially the styliform uropods, is so different from that seen in *A. stimpsoni* as to require, pending some future evidence to the contrary concerning thoracopods, a separate species for this material within the genus *Acanthotelson.*

The shorter and broader telson of *A. kentuckiensis* is more primitive than the long styliform tail of *A. stimpsoni.* Apparently, the styliform expression is allometric since the smallest specimen of *A. kentuckiensis,* SDSNH 23723, has the broadest and shortest telson (Table 1) while the larger specimens are narrower and longer. *A. stimpsoni,* by contrast, is a generally larger and more robust species than *A. kentuckiensis,* and has a very long, styliform telson.

The biota associated with *A. kentuckiensis* indicates a fresh to brackish water facies. In addition to occasional fish scales and teeth, abundant remains were collected of the pelecypod *Anthraconaia,* and fossils of the plant *Calamites* were common. These observations on the biota are reinforced by the nature of the black, fissile, canneloid shale in which the animals are found. The fossils occur at the base of a generally coarsening sequence of shales and sandstones, beginning with the carbonaceous shales with abundant fossils, and grading into an increasing arenaceous sequence with interbedded gray and black shales. These beds overlay another coarsening sequence with the River Gem

TABLE 1. Measurements in mm on material of *Acanthotelson kentuckiensis.* Comparative data on telson measurements included for two representative specimens of *A. stimpsoni,* see text for discussion. * Holotype.

Specimen	Length cephalon	Length A_1 peduncle	Length a_6	Length telson	Max. width telson	Ration tl:tw	Length uropodal exopod	Length uropodal endopod
A. kentuckiensis								
*SDSNH 23722	~3.0	1.8	0.9	3.2	1.0	3.2	4.0	3.3
SDSNH 23723			~0.5	1.5	0.8	1.9		2.4
SDSNH 23724			1.3	3.0	1.1	2.7		
SDSNH 23725			0.8	2.7	0.9	2.9		3.5
A. stimpsoni								
SDSNH 17454				7.5	1.7	4.4		
SDSNH 5210				7.1	1.6	4.4		

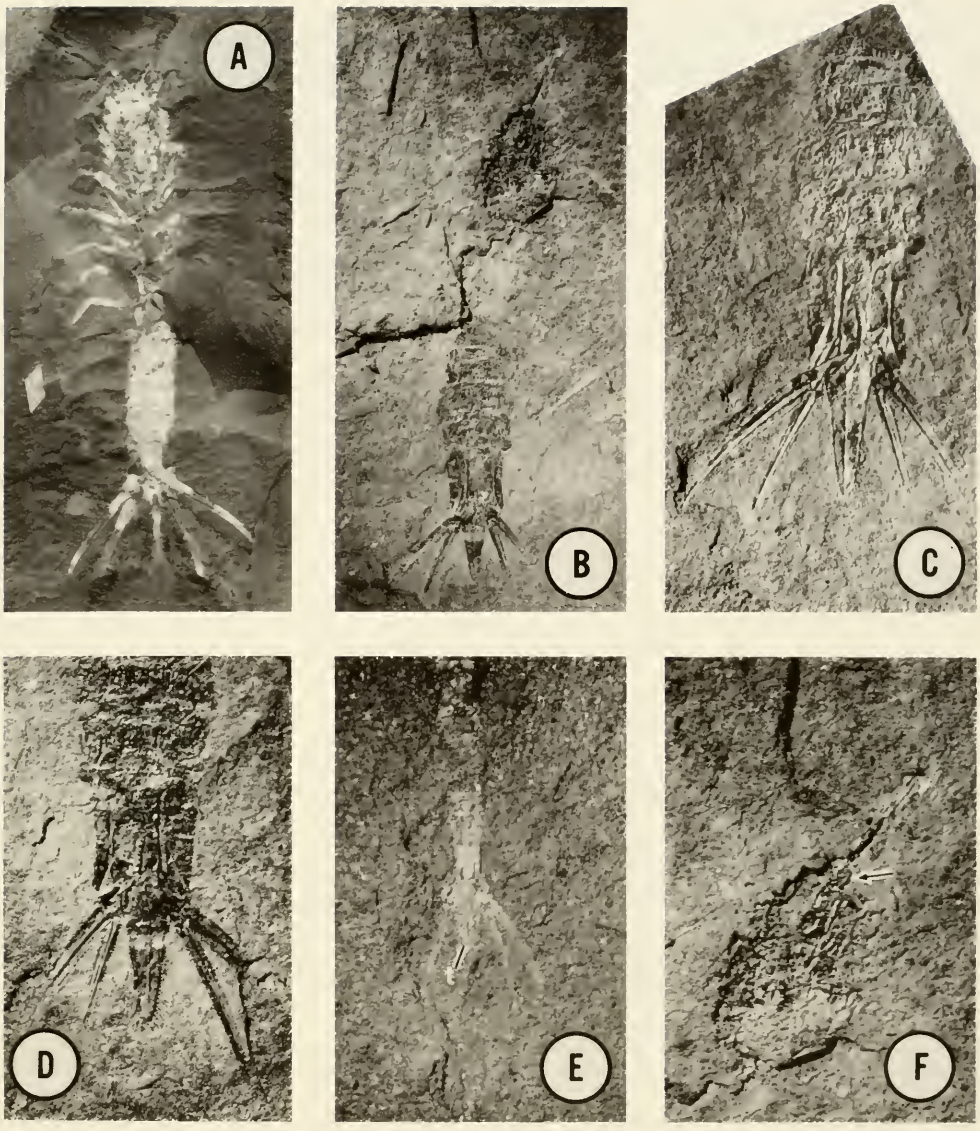


PLATE 2

FIGURE A. *Acanthotelson stimpsoni* Meek and Worthen, 1865, paralectotype X 344-Z, ×1.3.

FIGURES B–F. *Acanthotelson kentuckiensis* new species; B–D, F) holotype SDSNH 23722; B) whole specimen displaying cephalon and abdomen, thorax missing, ×3.9; C, D) closeup of tailfan counterparts, ×7.8; F) closeup of cephalon, note antennular peduncle with 3 subequal segments (arrow). E) SDSNH 23723, note relatively wider telson (t) in relation to length than that seen in C or D, ×6.

Rider Coal at the base, on top of which are a siltstone and shale grading into a heavy burrowed argillaceous sandstone.

Genus URONECTES Bronn, 1850 (=GAMPSONYCHUS Burmeister, 1855)

Diagnosis.—No rostrum. First thoracomere moderately reduced. Second thoracopod raptorial. Telson and uropods broad and rounded, uropods with straight diaeresis, broad tailfan formed from overlapping elements.

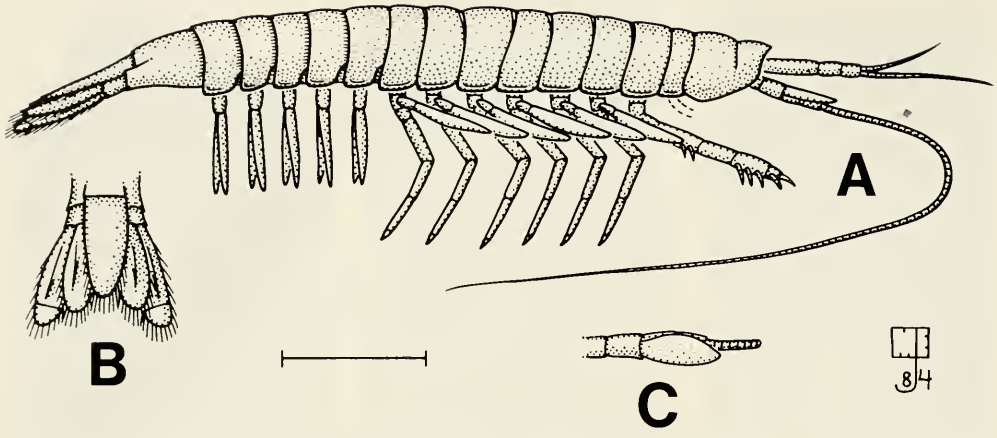


FIGURE 11. A) Reconstruction of *Uronectes fimbriatus,* scale 5 mm (modified and corrected from Brooks, 1962*b*); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

Type species.—*Gampsonyx fimbriatus* Jordan, 1847.

Uronectes fimbriatus (Jordan), 1847
Fig. 11

*1847 *Gampsonyx fimbriatus* Jordan, p. 89, pl. 2.
*1848 *Gampsonyx fimbriatus* Jordan. Bronn, p. 575.
*1850 *Gampsonyx fimbriatus* Jordan. Bronn, p. 575.
*1850 *Uronectes fimbriatus* (Jordan). Bronn, p. 575.
1854 *Gampsonyx fimbriatus* Jordan. Jordan & von Meyer, p. 1, pl. 2.
1855 *Gampsonychus fimbriatus* (Jordan). Burmeister, p. 191, pl. 10, figs. 12–14.
*1856 *Uronectes fimbriatus* (Jordan). Roemer, p. 202.
*1856 *Gamsonychus fimbriatus* (Jordan). Roemer, p. 202, p. 672.
1873 *Gampsonyx fimbriatus* Jordan. Feistmantel, p. 593, pl. 18, figs. 9–11.
1877 *Carcinurus fimbriatus* (Jordan). Goldenburg, p, 35, pl. 2, figs. 1b, 2–7.
1880 *Gampsonyx fimbriatus* Jordan. Brocchi, p. 10, pl. 10, fig. 7.
*1885 *Gampsonychus fimbriatus* (Jordan). Zittel, p. 672, fig. 857 (in part).
*1886b *Gampsonychus fimbriatus* (Jordan). Packard, p. 130, fig. 1.
1896 *Gampsonyx fimbriatus* Jordan. Calman, p. 798, pl. 2, fig. 17.
1900 *Gampsonyx fimbriatus* Jordan. Eastman in Zittel, p. 659, fig. 1382.
1901 *Gampsonychus fimbriatus* (Jordan). Fritsch, p. 72, pl. 159, text-fig. 377.
*1902 *Uronectes fimbriatus* (Jordan). Calman, p. 66.
1909 *Gampsonyx fimbriatus* Jordan. Smith, p. 568, fig. 53–55.
1916 *Gampsonychus fimbriatus* (Jordan). Vanhöffen, p. 143, fig. 7–8.
1927 *Uronectes fimbriatus* (Jordan). Haack, p. 733, 3 figs.
*1927 *Uronectes fimbriatus* (Jordan). Chappuis, p. 605.
*1931 *Uronectes fimbriatus* (Jordan). Van Straelen, p. 18.
*1958 *Uronectes fimbriatus* (Jordan). Malzahn, p. 355.
*1959 *Gampsonychus fimbriatus* (Jordan). Siewing, p. 1.
1962*a* *Uronectes fimbriatus* (Jordan). Brooks, p. 236.
1962*b* *Uronectes fimbriatus* (Jordan). Brooks, p. 230, text-pl. 11b.
*1963 *Uronectes* species. Noodt, p. 82.
1969 *Uronectes fimbriatus* Jordan. Brooks, p. R355, figs. 165-3, 173.
*1969a *Uronectes fimbriatus* Jordan. Schram, p. 221, table 1.
*1972 *Uronectes* species Jordan. Boy, p. 47, fig. 2.
*1974 *Uronectes fimbriatus* Jordan. Schram & Schram, p. 101.
*1979 *Uronectes fimbriatus* Jordan. Schram & Schram, p. 170.
*1982 *Uronectes* species Schneider, et al., p. 75, fig. 5.

Diagnosis.—Sixth thoracomere somewhat enlarged over adjacent segments. Sixth pleomere long.

Lectotype.—Jk 4a, b, from the Krämer Ironworks of Lebach, near Saarbrücken, Saarland, West Germany. Rotliegende, Lower Permian.

Paralectotype.—Jk 5.

Other localities.—Pfeffelbach, near Kusel, Rheinlandpfalz, West Germany; Rotliegende. Oberhof (Schweitzerhätte), near Zella-Mehlis, Thüringia, East Germany; Oberhöfer Beds, Lower Permian.

Diagnosis.—Cephalon with faint cervical groove, no rostrum. Antennule peduncles 3-segmented, proximal segment very long, distal 2 joints short, flagella moderately developed. Antennal protopod with 2 subequal segments, scaphocerite oval, flagellum moderately long with proximal 2 segments peduncular.

First thoracomere moderately reduced. Thoracic pleura simple, with slight furrow along margins. Sixth thoracomere somewhat longer dorsally than others. Second thoracopod large, spinose, and raptorial. Second through eighth thoracopods ambulatory, more or less subequal, ischium very short, merus through propodus moderate, dactylus very small.

First 5 pleomeres with finely serrate posterior margins, pleura acuminate anteriorly with slight furrow on margins. Sixth pleomere elongate. Telson rounded, margins setose. Uropods flap-like, margins setose, exopod with straight diaeresis and reinforced with lateral thickened rib.

Remarks.—The reconstructions of *U. fimbriatus* prepared by Brooks (1962*b*, 1969) generally reflect an accurate view of the creature, except for the fact that he mistakenly drew 7 abdominal segments instead of 6 (corrected here in Fig. 11). The description in his text indicates the proper number.

The classic Lebach locality has been the source of *U. fimbriatus* specimens in museums around the world. The freshly collected material was a black shale. The characteristic red rock with white fossils developed only after the specimens were "roasted" at the Krämer Ironworks, driving off the volatile organics in the shale and fossils, and leaving a calcitic residue behind on a rock residue high in siderite. Specimens from other localities were found by me while searching various European collections. The Staatssamlungen für Paläontologie in Munich has an "unroasted" specimen from the Rotliegende (BS 1975 I 164) from Pfeffelbach, near Kusel, not too far from Lebach. The Munich collection also has a specimen from the Oberhöfer Beds from near Oberhof, in Thüringia (BS 1953 XXVIII 21) in a strange 3-dimensional preservation. The Paläontologisches Museum of the Museum für Naturkunde in Berlin also has specimens (PMB A. 62–67) identified as *U. fimbriatus* from Thüringia (H.-E. Gruner, *pers. comm.*), as does the San Diego Natural History Museum (these a gift of Dr. J. Schneider of the Bergakademie, Freiberg).

Uronectes kinniensis Schram and Schram, 1979
Fig. 12

v.*1979 *Uronectes kinniensis* Schram and Schram, p. 169, pl. 1, text-fig. 1.
1981*a* *Uronectes kinniensis* Scharm and Schram. Schram, p. 133, text-fig. 4g.

Diagnosis.—Fourth thoracomere moderately reduced; eighth thoracomere with lateral semicircular ridges. Fifth pleomere elongate.

Holotype.—USNM 235625. Kinney Clay Pit, SE ¼, Sec. 18, T9N, R6E, Bernalillo County, New Mexico. Madera Formation, Virgilian, Pennsylvanian.

Description.—Cephalon apparently undecorated, no rostrum. Antennal protopod of 2 subequal segments, scaphocerite subtriangular and setose, at least proximal-most joint of flagellum peduncular.

First and fourth thoracomeres moderately reduced. All thoracomeres except eighth undecorated, pleura simple. Eighth thoracomere with small, lateral, paired, semicircular ridges. Thoracomeres 3 through 8 subequal (details obscure).

Pleopods with finely serrate posterior margins. Fifth pleomere elongate. Telson rectangular, rounded distally, and apparently distally serrate. Uropods as broad flaps, exopod with straight diaeresis, at least endopods setose.

Remarks.—The lack of knowledge about the first and second thoracopods makes it difficult to place this species in *Uronectes* without any hesitation. However, as orig-

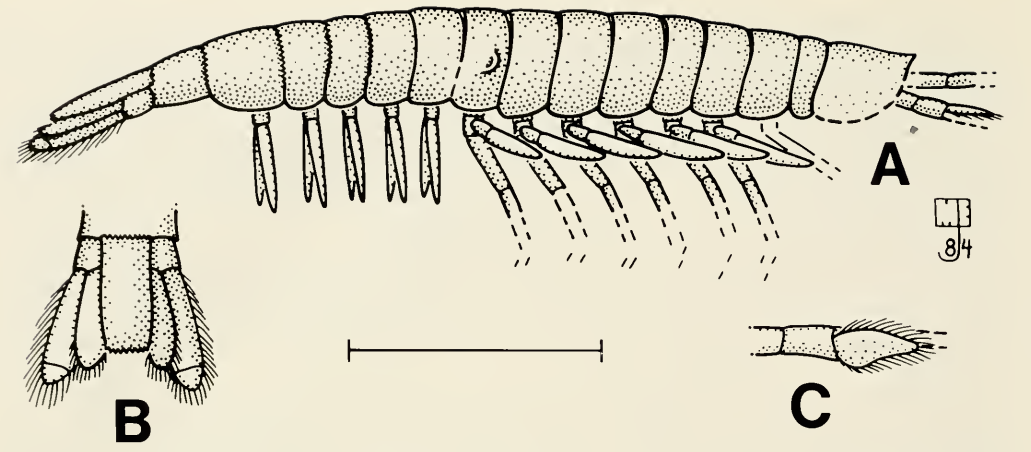


FIGURE 12. A) Reconstruction of *Uronectes kinniensis,* scale 5 mm (modified from Schram and Schram 1979); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

inally reported (Schram and Schram 1979:170) the overall aspects of the anatomy (especially the serrate pleomere margins, lack of rostrum, moderately reduced first thoracomere, and straight diaeresis) come closest to *Uronectes,* and *U. kinniensis* is best left within that genus for the time being.

Genus PALAEOSYNCARIS Brooks, 1962*b*

Diagnosis.—First thoracomere very reduced, second thoracomere moderately reduced. Second and third thoracopods raptorial. Telson oval, with spinose margins. Uropodal exopods laterally spinose.

Type species.—*Palaeosyncaris dakotensis* Brooks, 1962*b*.

Palaeosyncaris dakotensis Brooks, 1962*b*
Fig. 13; Plate 3, figs. B–E

v.*1962*b Palaeosyncaris dakotensis* Brooks, p. 251; pl. 65, figs. 3, 4, pl. 66; text-pl. 14, fig. a.
1969 *Palaeosyncaris dakotensis* Brooks. Brooks, p. R355, figs. 169–2, 170–2.

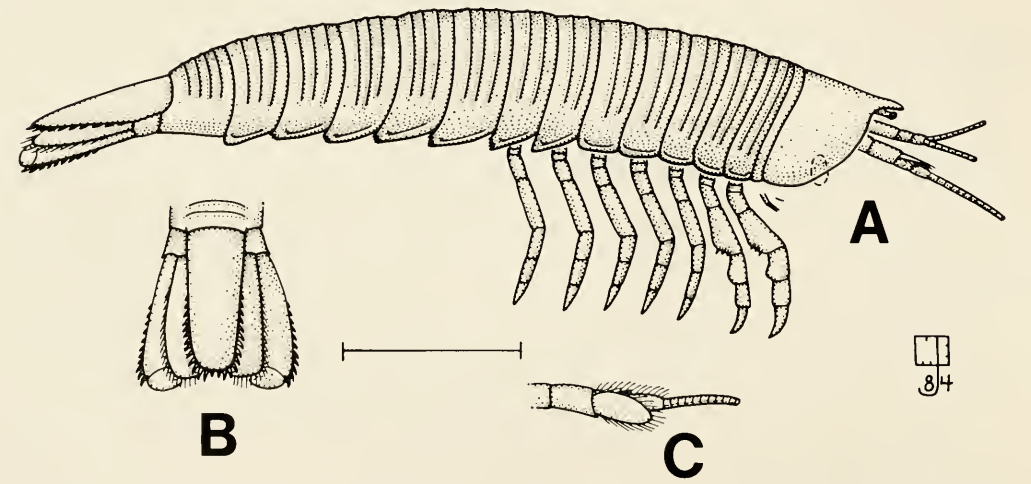


FIGURE 13. A) Reconstruction of *Palaeosyncaris dakotensis,* scale 5 mm (corrected from Brooks 1962*b*); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

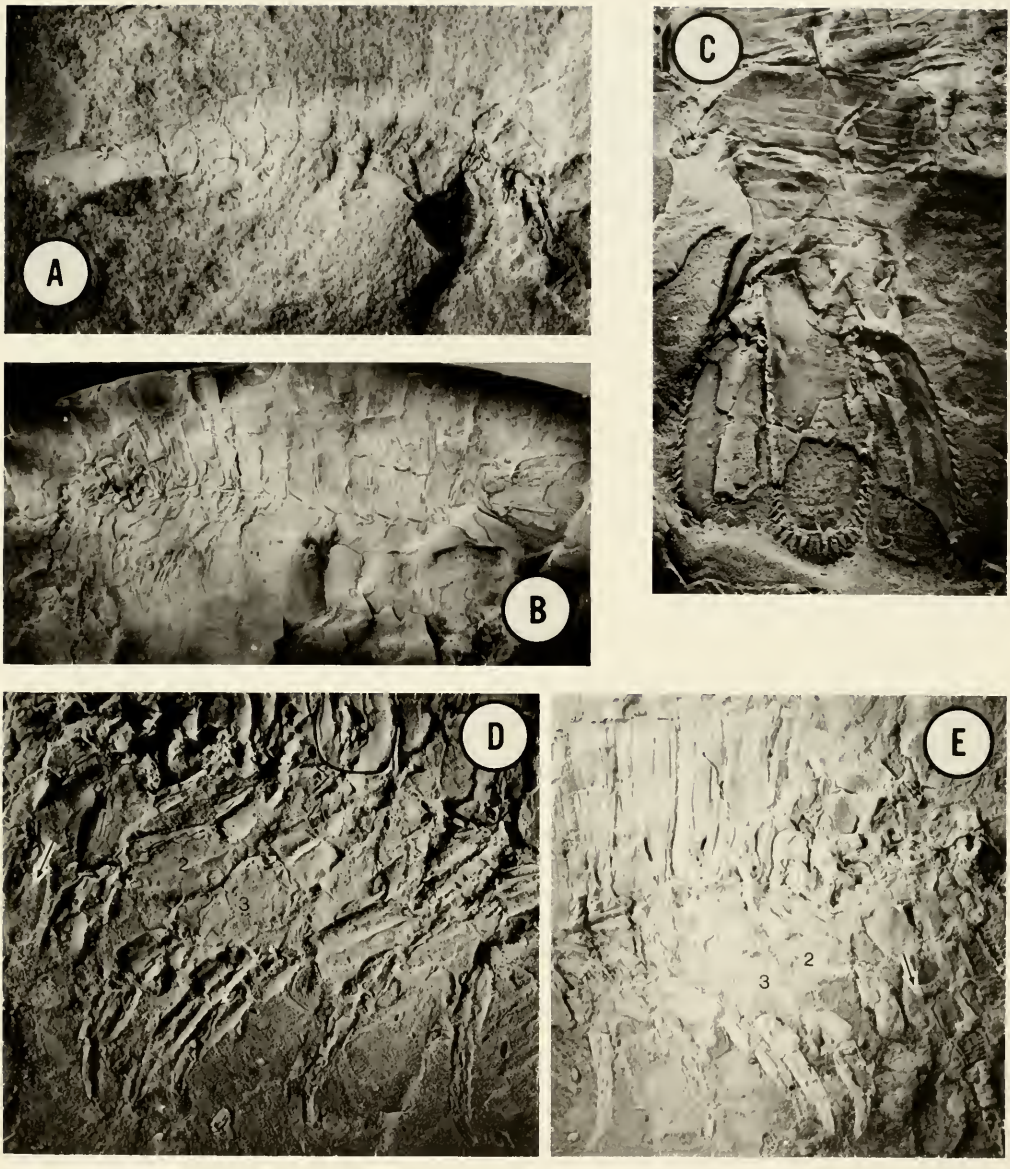


PLATE 3

FIGURE A. *Palaeosyncaris micra* new species, holotype, PE 2496, ×4.1.

FIGURES B–E. *Palaeosyncaris dakotensis* Brooks, 1962*b*; B–D) holotype, USNM 143409; B) whole specimen, ×2.4; C) closeup of tailfan, ×7; D) closeup of anterior thoracopods, note the inflated meri on thoracopods (2) and (3) and antennal scale (arrow), ×8; E) counterpart of holotype, Univ. of North Dakota collection, note inflated meri on thoracopods (2) and (3) and antennal scale (arrow), ×5.5.

1969a Palaeosyncaris dakotensis Brooks. Schram, p. 216, table 1.
1974 Palaeosyncaris dakotensis Brooks. Schram and Schram, p. 95.

Diagnosis.—All segments with transversely striate decoration. Abdominal pleura with posterior margins serrate.

Holotype.—USNM 14309 (Plate 3, figs. B–D) (counterpart, unnumbered, in collection of University of North Dakota, Plate 3, fig. E). Borehole Casimer Duletski No.

1, 8170–8180 feet NW ¼, NW ¼, Sec. 16, T139N, R99W, Stark County, North Dakota. Heath Shale, Upper Mississippian.

Description.—Eyes small, eye stalk long. Antennules with 3-segment peduncle, proximal joint equal to distal 2 joints, flagella well developed. Antennae with small, oval, finely setose scaphocerite, proximal 2 joints of flagellum peduncular with median margins setose, flagellum well developed (but of undetermined length).

First thoracomere greatly reduced, second thoracomere moderately reduced; second and all other somites (Plate 3, fig. B) with transverse striae, pleura rounded, and ventral margins with furrow. First thoracopod apparently reduced; second through eighth thoracopods robust, merus somewhat longer than other subequal joints, merus on second and third thoracopods (Plate 3, figs. D–E) inflated (possibly spinescent), dactylus long and pointed, second and third thoracopods raptorial. Eighth thoracic pleuron posteriorly extended and margin serrate. All tergites with marginal furrows, especially prominent on pleura.

Abdominal pleura anteriorly somewhat rounded, posteriorly pointed with margins serrate. Last pleomere somewhat elongate. Telson long, oval, and marginally spinose, terminal median spines reduced in comparison to adjacent members of series. Uropodal exopod laterally spinose, endopod margins finely setose (Plate 3, fig. C).

Remarks.—Though obviously well-preserved thoracic epipodites and exopods appear not to have been present on the type specimen, there is some indication on the coxa of the third thoracopod of USNM 143409 of a foramen for an epipodite. This same appendage may also preserve part of an exopod arising from the basis.

The thoracopodal endopods of this species are all strongly developed. The inflated meri on the second and third thoracopods may well have been capable of acting like subchelae in opposition to the carpi on these appendages, which appear to be proximally narrow and with a rather disto-posterior spiniform crest. In this regard USNM 143409 appears to have partially preserved the sockets of articulating spines on the merus of the second thoracopod disto-posteriorly.

Brooks (1962) compared *P. dakotensis* to *Praeanaspides praecursor,* mainly on the basis of similarities of tergal ornament. The tailfans, however, are now known to be quite different (Schram 1979*a*). Furthermore, the identification of raptorial thoracopods on *P. dakotensis* would appear to ally this species with members of the Acanthotelsonidae. Placement in this family should not be without query, however, since complete knowledge of the thoracic exopods and pleopods would be necessary before unquestioned affiliation could be sanctioned. Pleopods are not preserved on the type counterparts.

The other syncarid of the Heath Shale is *Squillites spinosus.* This latter species is collected from "paper shale" outcrops of the Heath in central Montana, while the rock of the North Dakota core which contains *P. dakotensis* is a well-indurated, blocky, black shale. The associated fauna on the core section with *P. dakotensis* is largely composed of partially pyritized cyzicoid branchiopods and casts of indeterminate ostracodes.

Palaeosyncaris micra. new species
Fig. 14; Plate 3, fig. A; Plate 4, figs. A–E

Diagnosis.—Body small. Segments mooth, undecorated. Abdominal pleura not serrate. Telson with spinose setae increasing in size distally.

Holotype.—PE 2496 (Plate 3, fig. A). Mazon Creek area; Will, Crundy, and Kankakee Counties, Illinois. Francis Creek Shale, Carbondale Formation (Westphalian C–D), Pennsylvanian.

Description.—Body small, tergites smooth. Cephalon with short rostrum. Antennules with 3 subequal joints in peduncle. Antenna with small setose scaphocerite.

First thoracomere greatly reduced, second moderately reduced, third through eighth subequal with anterior corners rounded (Plate 4, figs. A, C). First thoracopod reduced, about one-half the length of ambulatory thoracopods. Second and third thoracopods

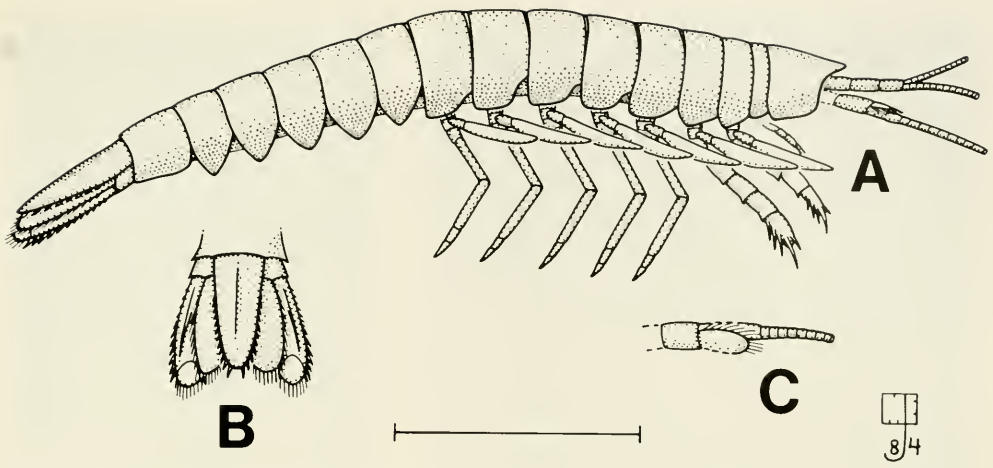


FIGURE 14. A) Reconstruction of *Palaeosyncaris micra,* scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

robust, raptorial, dactyli with well-developed terminal spines (Plate 4, fig. A). Third through eighth thoracopods ambulatory; meri and carpi long, ischia, propodi, and dactyli short; exopods flap-like (Plate 4, fig. C).

Abdominal pleura anteriorly and posteriorly reduced. Sixth pleomere somewhat longer than anterior pleomeres. Telson oval (Plate 4, fig. D), medial margins with spinose setae, with setae increasing in size distally. Uropods (Plate 4, figs. D, E) setose, setae of lateral margin of exopod spinose, exopod reinforced with medial rib and apparently possessing an oval diaeresis.

Remarks.—The small size and generally incomplete preservation of these fossils has resulted in their being mistakenly sorted by previous workers (including myself) as "small and poorly preserved" examples of the other two Mazon Creek syncarids, *Acanthotelson stimpsoni* and *Palaeocaris typus.* We are indebted to Mr. Stephen L. May for recognizing these specimens as a separate species, and bringing it to our attention. Representative measurements are given in Table 2.

The establishment of a third Mazon Creek syncarid now brings the crustacean assemblage of the brackish water biotope in the American Pennsylvanian into accord with that of the European Carboniferous (Schram 1981*a*). Both faunas now have a pygocephalomorph associated with 3 species of syncarid (see Table 3). However, there does not appear to be a point-for-point analogy between the syncarid species. The American faunas have 2 rapacious acanthotelsonids and 1 palaeocarid, whereas the British fauna syncarids are in apparently 3 different families. *Palaeosyncaris micra* occurs in both the Essex and Braidwood faunas of Johnson and Richardson (1966).

TABLE 2. Representative measurements in mm of species of *Palaeosyncaris.* * Holotypes.

	Head	Thorax	Abdomen	Telson	T_1	T_2	T_3	A_4
P. dakotensis								
*USNM 143409	3.5	10.5	11.0	4.0	0.6	1.1	1.3	2.5
P. micra								
*PE 2496	0.8	7.8	7.5		0.4	0.5	0.8	
PE 11670	~1.8	8.8			0.6	1.0	1.1	
PE 1268			7.1	2.6			0.8	1.2
PE 12174	1.0	7.9	7.0		0.4	0.7	0.9	1.1
PE 37912	1.0	6.8	5.5		0.4	0.6	0.8	
PE 37915	1.3	8.1			0.5	0.7	1.0	

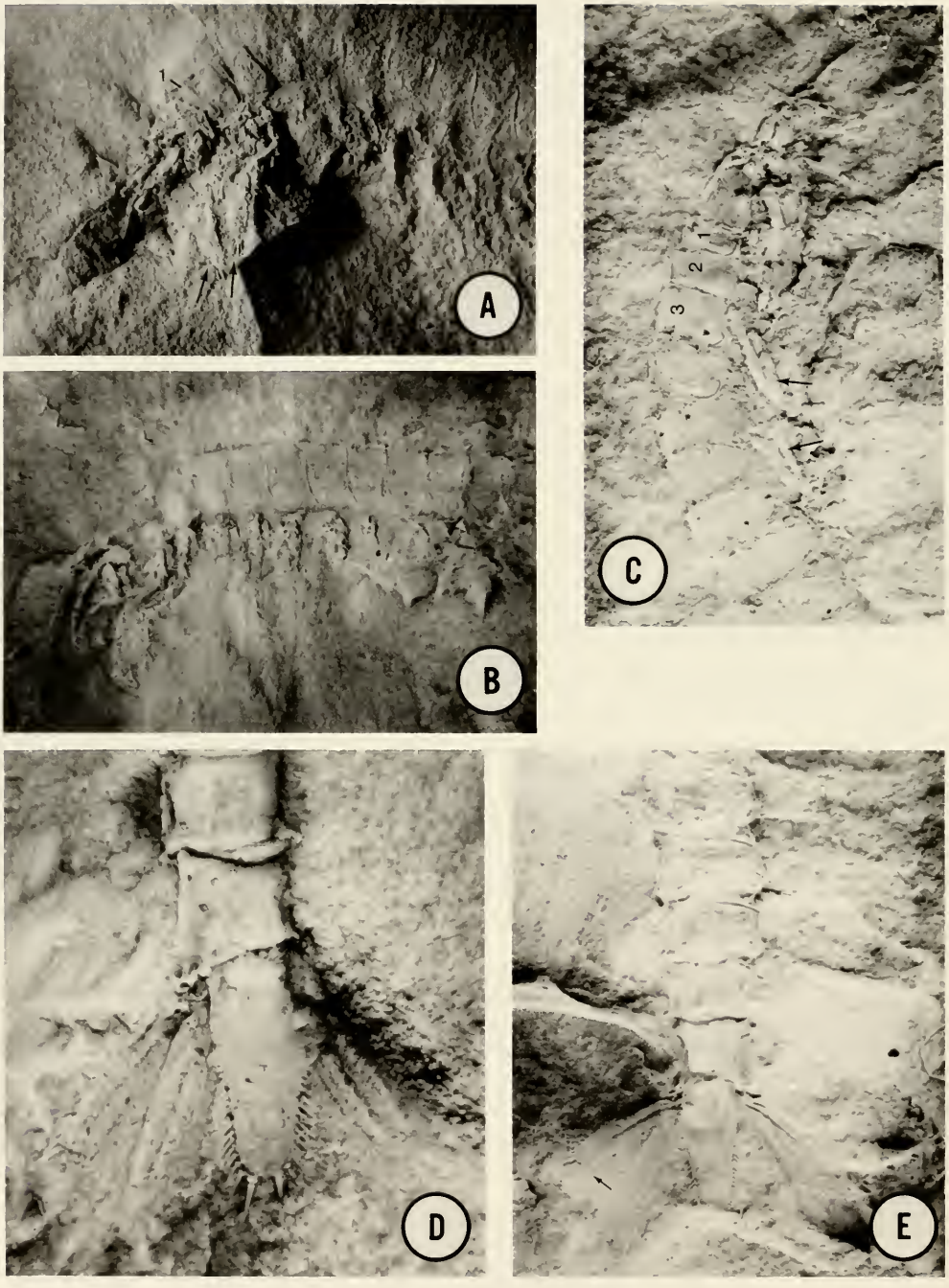


PLATE 4

FIGURES A–E. *Palaeosyncaris micra* new species; A) latex peel of holotype, PE 2496, closeup of anterior end, note the raptorial thoracopods 2 and 3 (arrows), and the reduced first thoracomere (1), ×9.8; B) latex peel of PE 11670, with rounded thoracic and abdominal pleura, ×4.5; C) latex peel of PE 37915, note progressively increasing lengths of anterior thoracomeres (1–3) and large flap-like exopods (arrows), ×7; D) latex peel of PE 12168, showing spination on telson, ×10.7; E) latex peel of PE 12174, showing spines on lateral margin of uropodal exopod and possible diaeresis (arrow), setation of endopod, and all but distal-most portions of the telson, ×7.4.

TABLE 3. Crustaceans found in Late Carboniferous brackish water habitats in North America and Europe.

	Mazon Creek Faunas	Westphalian British Coal Measures
Pygocephalomorpha	*Acanthotelson stimpsoni*	*Pygocephalus cooperi*
Syncarida	*Acanthotelson stimpsoni* *Palaeocaris typus* *Palaeosyncaris micra*	*Praeanaspides praecursor* *Palaeocaris retractata* *Pleurocaris annulatus*

Family PALAEOCARIDIDAE Meek and Worthen, 1865

Diagnosis.—Thoracic exopods flap-like, pleopods annulate.

Type genus.—*Palaeocaris* Meek and Worthen, 1865.

Remarks.—The genus *Paleocaris* has long been treated as a catchall taxon for every incompletely known Paleozoic eumalacostracan which has not had any evident carapace. This has been complicated by the fact that *Palaeocaris* itself was incorrectly understood, in the sense of Brooks (1962). Unfortunately, much remains to be discovered about this most important genus of Paleozoic syncarids; however, the diagnostic combination of annulate pleopods with flap-like thoracic exopods provides a focus upon which further work in the group can be based. It is possible the genera *Brooksyncaris, Palaeorchestia,* and *Williamocalmania* may belong to this family, but these fossils yet lack relevant information about the appendages to allow definitive placement of them into the Palaeocarididae.

Genus PALAEOCARIS Meek and Worthen, 1865

Diagnosis.—Mandibles massive, first thoracomere greatly reduced. Sixth pleomere posterior margin deeply concave. Uropodal rami margins very setose, exopod with pronouced diaeresis, exopod distinctly longer than endopod, endopod distinctively longer than telson. Telson oval, margins bearing stout setae.

Palaeocaris typus Meek and Worthen, 1865 [=*Acanthotelson inaequalis* Meek and Worthen, 1865]

Fig. 15; Plate 5, figs. A–C

1865 *Acanthotelson inaequalis* Meek and Worthen, p. 48.
v.*1865 *Palaeocaris typus* Meek and Worthen, p. 49.
1866 *Acanthotelson inaequalis* Meek and Worthen. Meek and Worthen, p. 403, pl. 32, fig. 7.
v. 1866 *Palaeocaris typus* Meek and Worthen. Meek and Worthen, p. 405, pl. 32, figs. 5, 5a–d.
1868*a* *Palaeocaris typus* Meek and Worthen. Meek and Worthen, p. 28.
1868*b* *Palaeocaris typus* Meek and Worthen. Meek and Worthen, p. 552, figs. 1, 2.
1880 *Palaeocaris typus* Meek and Worthen. Brocchi, p. 9, pl. 1, figs. 8–10.
1884 *Palaeocaris typus* Meek and Worthen. White, p. 179, pl. 38, figs. 1–3.
v. 1886*b* *Palaeocaris typus* Meek and Worthen. Packard, p. 129, pl. 7, figs. 1–2.
1889 *Palaeocaris typus* Meek and Worthen. Packard, p. 213.
1896 *Palaeocaris typus* Meek and Worthen. Calman, p. 796, pl. 2, fig. 15.
1909 Palaeocaris typus Meek and Worthen. Smith, p. 570, text-figs. 56–58.
1916 Palaeocaris typus Meek and Worthen. Vanhöffen, p. 141, fig. 5.
1916 Acanthotelson inaequalis Meek and Worthen. Vanhöffen, p. 147.
1927 Palaeocaris typus Meek and Worthen. Chappuis, p. 605.
v? *1957a Palaeocaris* species. Copeland, p. 595; pl. 6, fig. 5.
v? *1957b Palaeocaris* cf. *typus* Meek and Worthen. Copeland, p. 47; pl. 15, fig. 1.
1959 Palaeocaris typus Meek and Worthen. Siewing, p. 3.
1959 Acanthotelson inequalis Meek and Worthen. Siewing, p. 102.
1961 Palaeocaris typus Meek and Worthen. Rolfe, p. 548.
v. 1962*b* *Palaeocaris typus* Meek and Worthen. Brooks, p. 240, pls. 60–64, text-pls. 12 (fig. a), 13.
1965 Palaeocaris species Noodt, p. 82.
1969 *Palaeocaris typus* Meek and Worthen. Brooks, p. R348, figs. 165-1, 167, 170-1a, 171.
1969a Palaeocaris typus Meek and Worthen. Schram, p. 219, table 1.
1969b Palaeocaris typus Meek and Worthen. Schram, p. 201.
1972 Palaeocaris typus Meek and Worthen. Secretan, p. 3.

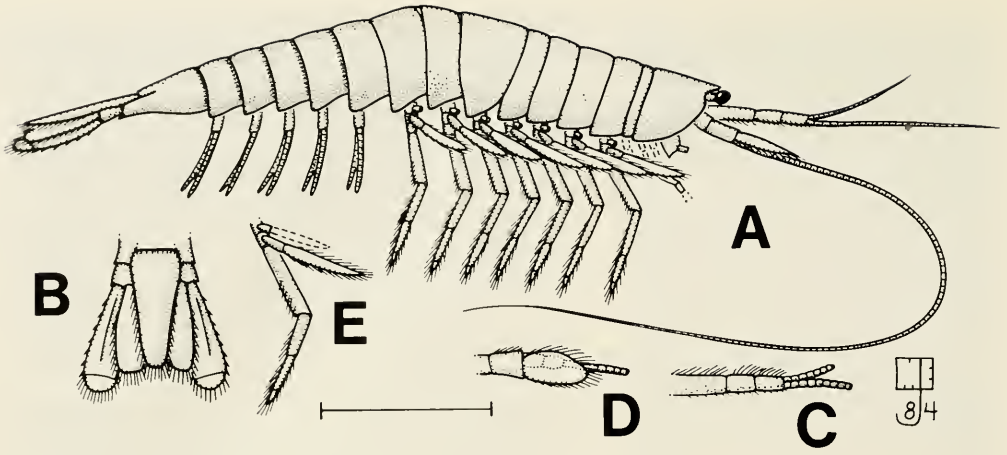


FIGURE 15. A) Reconstruction of *Palaeocaris typus,* (corrected from Brooks 1962*b*), scale 5 mm; B) tailfan to same scale as body; dorsal views of right C) antennule and D) antenna; E) posterior thoracopod. Appendages slightly enlarged.

1974 Palaeocaris typus Meek and Worthen. Schram and Schram, p. 101.
1976a Palaeocaris typus Meek and Worthen. Schram, p. 21.
1976b Palaeocaris typus Meek and Worthen. Schram, p. 411.
1978 Palaeocaris typus Meek and Worthen. Schminke, p. 235, fig. 17.
1979a Palaeocaris typus Meek and Worthen. Schram, p. 28, table 1.
1979b Palaeocaris typus Meek and Worthen. Schram, p. 167, table 2.
1981*a Palaeocaris typus* Meek and Worthen. Schram, p. 131, text fig. 5c, table 2.
1981*b Palaeocaris typus* Meek and Worthen. Schram, p. 9, fig. in text.

Diagnosis.—Head to thorax ratio 1:4. Scaphocerite longer than the two peduncular segments of antennal flagellum. Sixth thoracomere larger dorsally than any other thoracomere. Uropodal diaeresis slightly curved to straight, outer margin of exopod with widely spaced spinose setae along its length terminating in 3 spines just anterior to diaeresis. Telson ovoid but wider proximally than distally.

Holotype.—X338 (Plate 5, fig. A), Mazon Creek area, Will County, Illinois. Francis Creek Shale, Carbondale Formation (Westphalian C), Pennsylvanian. [Brooks (1962*b*: 248) states that the types of this species "are misplaced or lost." However, close comparison of X338 with the description of Meek and Worthen (1868, fig. A:552), and the more detailed treatment in their original description (Meek and Worthen 1865), reveal that this specimen was undoubtedly the basis for these texts and the 1868 illustration, and is thus almost certainly the holotype.]

Other localities.—Abandoned Chieftan Mine, 7 miles south of Terra Haute, Indiana, east of Highway US-41; Lower Shelburn Formation, Pennsylvanian. Abandoned strip mine talus 1.8 miles west of Windsor, Missouri, on Highway MO-2.

Description.—Cephalic shield smooth, except for slight lateral groove at level of mandible. Rostrum small. Optic notch prominent. Ventral margins of cephalic shield rounded and whole. Eyes moderate in size, stalk with prominent (peracarid-like) papilla. Antennular peduncle 3-segmented, proximal-most joint as long as distal 2 joints, medial margins setose, inner flagellum shorter than outer flagellum, outer flagellum about one-third body length. Antennal protopod with short proximal joint and large distal joint, scaphocerite oval and setose, 2 basal flagellar joints peduncular, medial margins of peduncular joints setose, flagellum equal to body length. Mandible massive, prominently projecting below cephalic shield margin, palp of at least 2 segments. Maxillules and maxillae with palps (details uncertain).

First thoracomere markedly reduced, sixth thoracomere larger than any other. Thoracic pleura broadly rounded anteriorly, posterior margin straight. First thoracopod

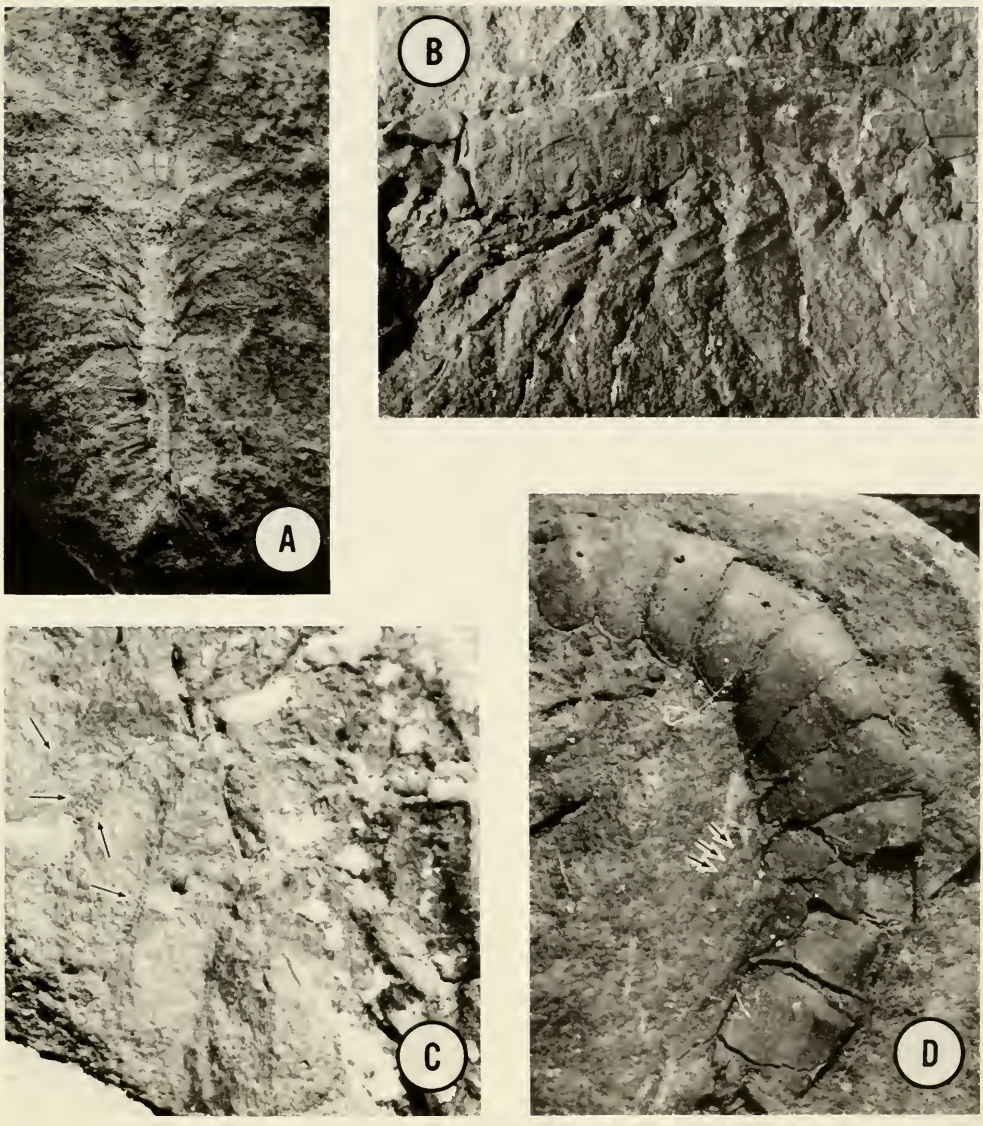


PLATE 5

FIGURES A–C. *Palaeocaris typus* Meek and Worthen, 1865; A) latex peel of holotype, X 388, ×1.9; B) YPM 19765, showing the flap-like thoracopodal exopods, ×4.5; C) PE 23237, showing annulate pleopods (arrows), ×8.9.

FIGURE D. *Palaeocaris retracta* Calman, 1932, I 13971, with short section of an annulate pleopod (arrow), ×6.7.

about one-half the size of succeeding appendages. Thoracopods 2 through 8 subequal, epipods present (details not known), exopods broadly flap-like (Plate 5, fig. B) and setose, endopods with short ischia and dactyli, meri and carpi long and subequal, propodi one-half the length of carpi.

Pleomeres with posterior margins finely setose, pleura of first 5 abdominal segments as in thoracomeres. Pleopods annulate (Plate 5, fig. C) [not flap-like as reported by Brooks 1962]. Telson oval, somewhat wider anteriorly than medially or posteriorly, margins with strong setae. Uropods flap-like, faint median reinforcing rib on setose

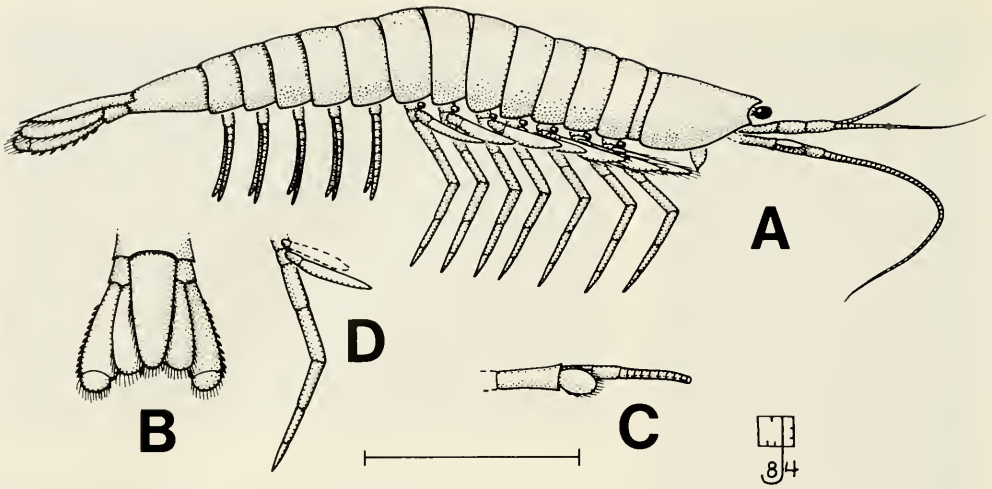


FIGURE 16. A) Reconstruction of *Palaeocaris retractata,* (modified from Schram 1979*a*), scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna; D) thoracopod. Appendages slightly enlarged.

rami, exopods with lateral margin spinose, setae distally developed as 3 small spines just anterior of straight to slightly curved diaeresis.

Remarks.—Brooks (1962*b*) made some errors in anatomical interpretation of the *P. typus* specimens available to him. He felt the antennal peduncle had 5 segments, 2 protopodal and 3 flagellar. The mistake arose in interpreting a preservation anomaly on the distal protopodal joint, mistaking a longitudinal crack in that joint for a longitudinal suture.

More importantly, Brooks reconstructed the pleopods of *P. typus* as flap-like, and compared them to those of *Acanthotelson stimpsoni.* The pleopods are rarely well-preserved on *P. typus.* The thoracic exopods are clearly flap-like (e.g., YPM 19765, Plate 5, fig. B). The pleopods, however, are annulate [YPM 19731, YPM 19765, PE 23237 (Plate 5, fig. C), PE 37893, PE 37957, PE 37976]. It is the correction of our understanding of this feature and its detection on other species of *Palaeocaris* that delineates the family Palaeocarididae from other palaeocaridacean syncarids.

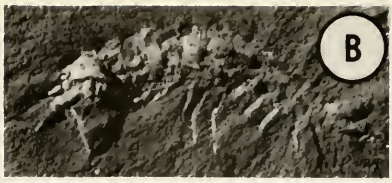
Palaeocaris retractata Calman 1932
Fig. 16; Plate 5, fig. D; Plate 6, fig. A

v. 1911*b* *Palaeocaris praecursor* (Woodward). Calman, p. 488, figs. 1, 2a, 3.
v. 1914 *Palaeocaris* species. Peach, p. 146, pl. 4, fig. 9.
*1932 *Palaeocaris retractata* Calman, p. 541.
1959 Palaeocaris retractata Calman. Siewing, p. 101.
v. 1961 *Palaeocaris retractata* Calman. Rolfe, p. 546, pl. 68, fig. 8, text-fig. 1.
1962b Palaeocaris retractata Calman. Brooks, p. 248.
1979*a* *Palaeocaris retractata* Calman. Schram, p. 106, figs. 50, 51.
1979b Palaeocaris retractata Calman. Schram, p. 170, table 2.
1981a Palaeocaris retractata Calman. Schram, p. 131, text fig. 5e, table 2.
1982 Palaeocaris retractata Calman. Schram, p. 123, fig. 8.

Diagnosis.—Head to thorax ratio 1:2.8. All thoracic segments subequal. Uropodal diaeresis a rounded to sigmoid curve, outer margin of exopod armed with spines. Telson ovoid, margin with spinose setae.

Holotype.—In 29012. Clay Craft open works, Cosely near Dudley, Worcestershire. Ten foot Ironstone Measures, Lower Similis-Pulchra Zone, Middle Coal Measures.

Other locality.—West flank Bilberry Hill, in Lickey Hills southwest of Birmingham, Warwickshire; Keele Beds, Westphalian D.



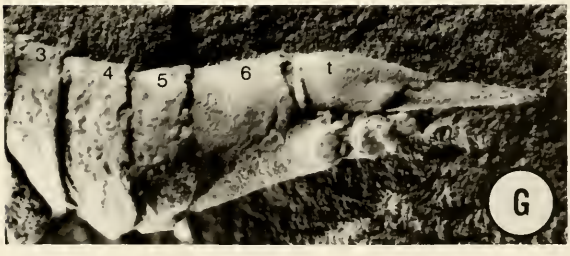


PLATE 6

FIGURE A. *Palaeocaris retractata* Calman, 1932, I 13973, showing setose margins of telson, ×7.

FIGURES B–G. *Palaeocaris secretanae* new species; B) holotype, AM 7423, ×3.6; C) AM 7243, closeup of cephalon, showing stalked eyes, bases of antennules and antennae, and mouthparts, ×10.7; D) AM 4293, closeup of annulate pleopod, ×22.3; E) AM 7861, showing optic notch, cephalic groove, large mandible, and thoracopodal exopods, ×10.7; F) AM 5019, showing cephalic groove and the markedly reduced first thoracomere, ×10.7; G) AM 7810, lateral preservation of posterior abdomen, with telson (t) and pleomeres (numbered), ×10.7.

FIGURE H. *Nectotelson krejcii* (Fritsch) 1875, B 77621, tailfan, ×6.6.

Descriptions.—Cephalic shield smooth, slight lateral groove at level of mandible, premandibular portion of cephalon as long or longer than the posterior region. Rostrum small. Optic notch slight. Eyes small to medium in size. Antennular peduncle with 3 subequal joints, the most proximal with an optic fossa. Antennal protopod with distal joint long, scaphocerite small and oval, 2 basal-most joints of flagellum peduncular. Mandible large with prominent incisor process.

All thoracomeres, except the markedly reduced first, subequal in length. Second through fourth thoracic pleura subquadrangular, posterior pleura broadly rounded anteriorly, all pleura with slightly marginal furrows. Second through eighth thoracopods with epipods possibly flap-like, moderate flap-like exopods, endopodal joints subequal with a tendency to shorten as one proceeds distally.

Second through sixth pleomeres with setose posterior margins. Pleopods annulate (Plate 5, fig. D). Telson oval, margins setose (Plate 6, fig. A). Uropodal exopod with rounded to sigmoid diaeresis, lateral margins spinose, other margins of rami setose (at least distally).

Remarks.—Reexamination and preparation of available material, In 29013, In 29014, and especially I 13971 (Plate 5, fig. D), indicates that the pleopods of *P. retractata* are annulate. This was not noticed in the redescription of Schram (1979*a*).

Now that other species of *Palaeocaris* are better understood, the large cephalon (small head to thorax ratio) is seen as quite diagnostic for this species. Other species, *P. typus* and *P. secretanae,* have relatively smaller heads.

Restudy in July of 1980 of all *P. retractata* material mentioned in Schram (1979*a*) allowed me an opportunity to reconsider the identity of doubtful specimens in light of these collateral studies of all fossil syncarids. I now feel that an incomplete specimen, GSL RAE 1291, is not an example of *P. retractata.* This correction does not affect our understanding of the anatomy of this species. However, it does shorten the biostratigraphic range of *P. retractata* (Schram 1979*a*:7, fig. 1), now understood to extend only from Westphalian B to D, i.e., from the Lower Similis–Pulchra Zone up into the Tenuis Zone.

Palaeocaris secretanae new species

Fig. 17; Plate 6, figs. B–F; Plate 7, figs. A & B

v. *1980a* palaeocarid syncarid. Secretan, p. 24, pl. 1.
v. *1980a* ?ceratiocarid phyllocarid. Secretan, p. 28, pl. 2, figs. 1, 2.
v. *1980a* ?eocaridacean. Secretan, p. 28, pl. 3, figs. 2, 3.
v. *1980a* pygocephalomorph. Secretan, p. 30, pl. 3, figs. 5, 6.
v. *1980a* ?palaeostomatopod. Secretan, p. 30.
v. *1980a* "specimens enigmatiques." Secretan, p. 32, pl. 4, figs. 2 & 6.
1980b Palaeocaris. species. Secretan, p. 414, pls. 1–4, fig. 1.
1981 Palaeocaris cf. *P. retractata* Calman. Pacaud et al., p. 40.
1982 Palaeocaris cf. *P. retractata* Calman. Rolfe et al., p. 426.

Diagnosis.—Head to thorax ratio 1:4.6. All thoracic segments subequal. Uropodal diaeresis markedly circular, outer margin of exopod armed with small spines distally near diaeresis, margins of rami with long dense setae, rami reinforced with heavy median ribs. Telson ovoid with distal end blunt, margin with long spines.

Holotype.—AM 7423–24 (Plate 6, figs. B & C). From shales above First Blanzy-Montceau Coal (=Puits St. Louis), Stephanian B, Upper Carboniferous. St. Louis open cast mine, Montceau-les-Mines, France.

Etymology.—Named in honor of Dr. Sylvie Secretan, who first recognized the nature and significance of this material, and who has been a major figure in organizing and coordinating the scientific study of the important biota of the Montceau-les-Mines locality.

Description.—Cephalic shield smooth, slight lateral groove at level of mandible (AM 5019; 7861, Plate 6, figs. E & F). Rostrum small to moderate in size. Optic notch prominent (AM 7861). Eyes moderate to large (AM 7423–24). Antennular peduncle with 3 subequal segments, median margins setose (AM 6137–38), flagella well developed

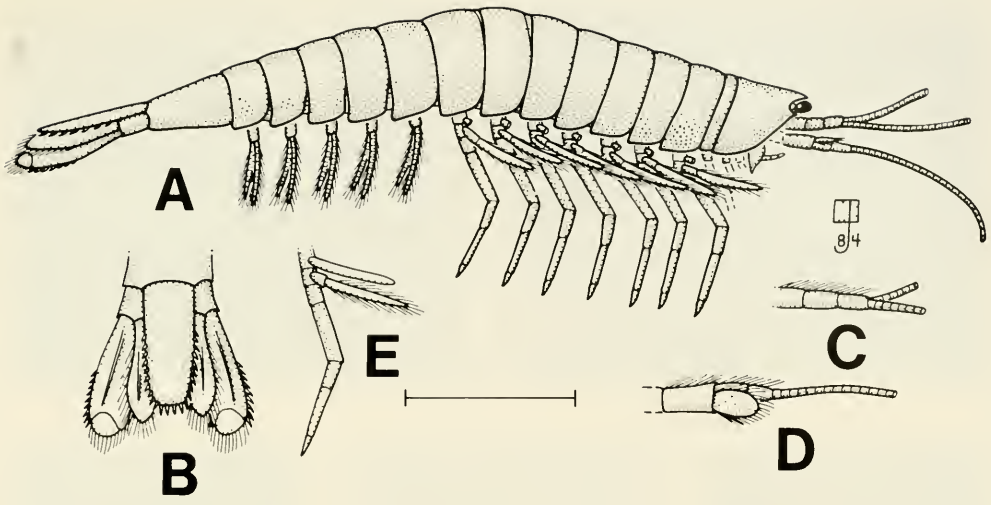


FIGURE 17. A) Reconstruction of *Palaeocaris secretanae,* scale 5 mm; B) tailfan to same scale as body; dorsal views of C) antennule and D) antenna; E) thoracopod. Appendages slightly enlarged.

(but of undetermined length). Antennal protopod with median margins setose (AM 7794), scaphocerite oval, small in size and setose, 2 proximal-most joints of flagellum peduncular and very large (AM 7524). Mandible (AM 5744) with large incisor process and well-developed palp.

Thoracic and abdominal pleura with gently rounded anterior corners and well-developed posterior corners (AM 7810, Plate 6, fig. G), all body segments (except first) subequal. First thoracopod reduced in size (AM 5019). Second through eighth thoracopods with long cylindrical epipodites (AM 7861), exopods large and flap-like with setose margins, endopodal ischium and dactylus small, merus and propodus long, and carpus moderate in length (AM 7423–24).

Annulate pleopods setiferous (AM 4293, Plate 6, fig. D; 4377, 7424). Telson with margin spinose (AM 7436, Plate 7, fig. B). Uropodal rami spatulate (AM 5080, Plate 7, fig. A), reinforced with strong median ribs, exopodal lateral margin with small spines distally (AM 5080), diaeresis strongly circular (Plate 7, fig. B), ramal margins with dense array of long setae.

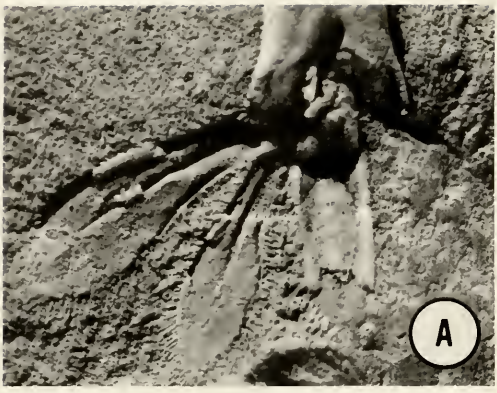
Remarks.—Though closely resembling *P. retractata, P. secretanae* is easily distinguished by its short cephalon (shorter than that of any species of *Palaeocaris*) and the spatulate nature of the uropodal rami, i.e., more narrow proximally than distally.

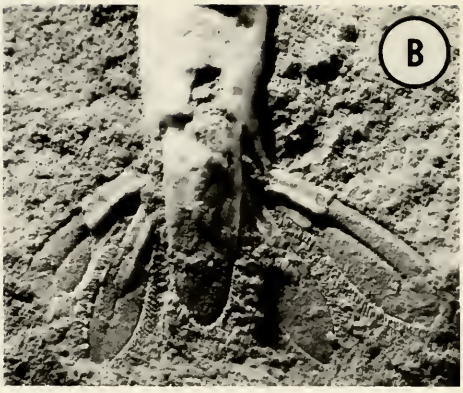
Although the general preservation of most of the material of *P. secretanae* is exceptionally fine, those specimens that were not so well-preserved can be rather confusing to interpret. This accounts for the variety of tentative assignments made by Secretan (1980*a, b*). Her non-syncarid identifications are all based on poorly preserved specimens. In point of fact, though the biota at Montceau-les-Mines is among the most diverse in the Carboniferous, *P. secretanae* remains the only malacostracan presently known from that fauna, save for one specimen that is possibly a phreatoicid isopod. Measurements comparable to those made by Brooks (1962b) on *P. typus* are provided in Table 4.

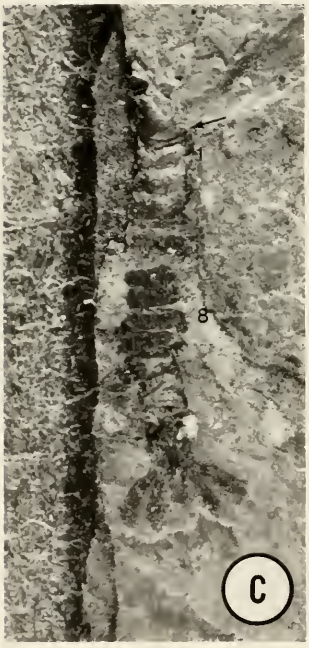
Family SQUILLITIDAE Schram and Schram, 1974

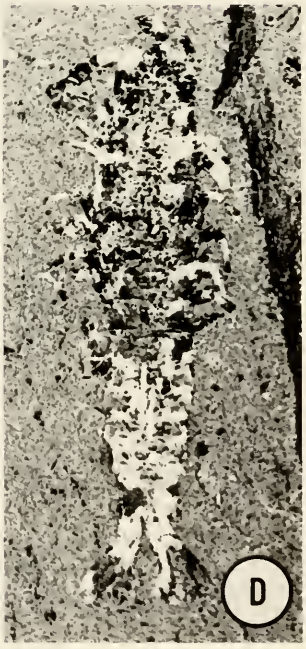
Diagnosis.—Thoracic exopods annulate, pleopods annulate and either uni- or biramous.

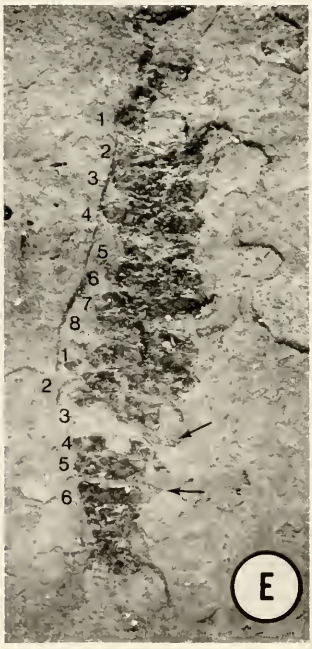
Type genus.—*Squillites* Scott, 1938.











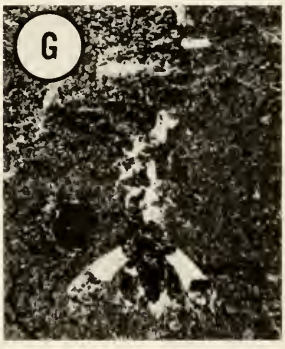


PLATE 7

FIGURES A & B. *Palaeocaris secretanae* new species; A) AM 5080, tailfan, ×10.7; B) AM 7436, tailfan, ×10.7.

FIGURES C–G. *Nectotelson krejcii* (Fritsch) 1875; C) B 7762b, showing prominent cephalic groove (arrow) and 8 subequal thoracomeres (numbered), ×5.6; D) M 1042, typical form and preservation of Czech localities, ×7; E) B 7762i, showing subequal trunk segments (numbered) and fragments of annulated pleopods (arrows), ×7; F) B 7762d, latex peel showing antennae and thoracopodal endopods, ×6.7; G) M 1033, showing setose margins of telson, ×5.

TABLE 4. Representative length measurements in mm of species of *Palaeocaris.** Holotype.

	Cephalon	Thorax	Abdomen	T_6	A_2	A_6	Telson	Body
P. secretaneae								
AM 3424	1.8	8.3		1.2	0.9			
4293	1.5	7.7		1.3	1.1			
4301–02			9.4		1.4	2.4	2.7	
4385–86	1.6	6.8		1.1				
4800							2.5	
5019	1.5	6.3						
5032–33	1.6	10.0	8.1	1.4	1.2	1.8		
5080			6.8					
5610–11						1.8	2.3	
5616	2.0							
5617	2.5							
5744	1.4	6.4	4.4			1.0		
7103–04			3.9		0.7	1.0		
7352	1.5	7.8		1.0				
7372–73			5.4	0.8	0.8	1.5		
7420	2.0	8.0			0.9			
*7423–24	1.5							
7427–28						2.0		
7429–30	1.3							11.5
7436					1.4	2.3		
7440			7.8		1.4	1.9	2.3	
7454–55							2.8	
7528			5.1		0.8	1.3		
7534	1.4	5.4		0.8	0.5			
7556	1.1	5.0	4.2	0.7	0.6	1.2		10.0
7766–67			4.5		0.7	1.2		
7794		9.3	7.5					
7810							3.2	
7845						1.8	2.2	
7861	2.3	10.2	7.8	1.5	1.4	1.9		20.0
8236			5.9			1.5		11.8
8338–39							1.9	
$\bar{x}$	1.67	7.6	5.9	1.1	1.0	1.6	2.5	13.3
P. typus $\bar{x}$	2.3	9.3		2.2	1.2	1.9	3.6	20.4
P. retractata $\bar{x}$	2.0	5.8	5.3				3.4	

Remarks.—Together the annulate thoracic exopods and pleopods of these species most resemble those seen in the living Anaspididae within the order Anaspidacea. However, the first thoracomere is not fused to the cephalon in these fossils: equal in size to all other thoracomeres in *Nectotelson,* slightly reduced in *Squillites,* and greatly reduced in *Praenaspides.*

Genus SQUILLITES Scott, 1938

Diagnosis.—First thoracomere only slightly reduced. Uropods narrow, spatulate, and setose. Telson subtriangular, armed with moveable spines.

Type species.—*Squillites spinosus* Scott, 1938.

Squillites spinosus Scott, 1938
Fig. 18

v.*1938 *Squillites spinosus* Scott, p. 508, figs. 1, 2.
1939 Squillites spinosus Scott. Berry, p. 467.
1962*b Squilites spinosus* Scott. Brooks, p. 254, pl. 53, figs. 1, 3; text-pl. 14, fig. d.
1965 Squillites species. Noodt, p. 82.
1967 Squillites spinosus Scott. Secretan, p. 173, fig. 8.
1969 *Squillites spinosus* Scott. Brooks, p. R355, figs. 169-1 and 170-3.
1969a Squillites spinosus Scott. Schram, p. 216, table 1.
v. 1974 *Squillites spinosus* Scott. Schram and Schram, p. 96, pls. 1–2, text-figs. 1, 2.

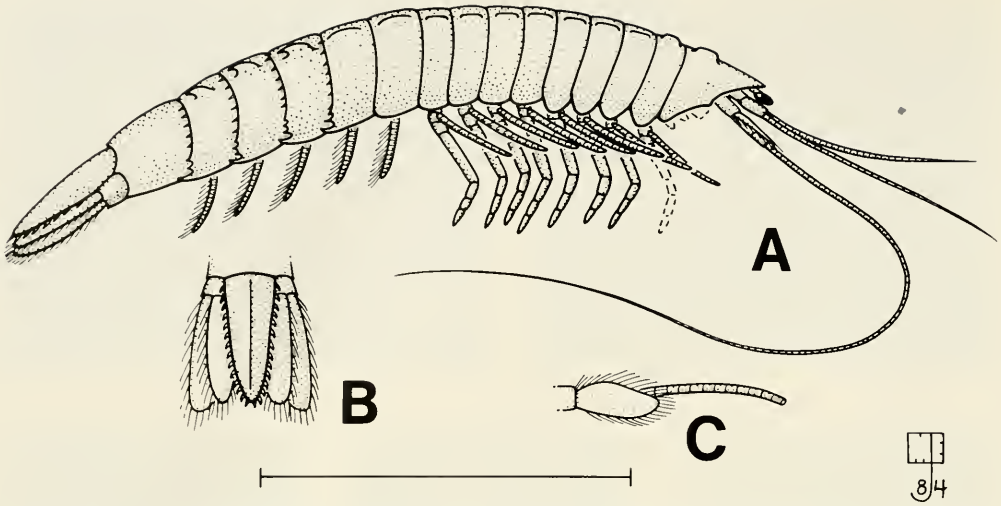


FIGURE 18. A) Reconstruction of *Squillites spinosus,* (modified from Schram and Schram 1974), scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

1979a Squillites spinosus Scott. Schram, p. 114.
1981 Squillites spinosus Scott. Schram, p. 133, text-fig. 4.
1982 Squillites spinosus Scott. Schram, p. 122.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Holotype.—X1219. One-half mile south of Heath, Fergus County, Montana; Heath Shale, Big Snowy Group, Upper Mississippian.

Description.—Stalked compound eyes small and spherical. Antennule with 3-segment peduncle, flagella long. Antennal protopod with only 1 segment observed, scaphocerite oval and setose, very long flagellum with proximal 2 segments large and peduncular. Cephalon with marked broad rostrum, lacking any cervical grooves, pair of semicircular mid-dorsal ridges.

Thoracomeres with 4 anterior pleura medially pointed and 4 posterior pleura rounded, pair of semicircular ridges mid-dorsal on each thoracomere, first thoracomere slightly shorter than others. Thoracopods subequal, ischia short and equal to bases, meri long, carpi through dactyli short.

Pleomeres variously decorated, first through fifth with setose posterior margins, first and second with mid-dorsal paired semicircular ridges, and third through fifth with large immobile posteriorly directed spines. First pleuron rounded, second through fifth pleura with posterior corners denticulate. Setose pleopods robust and uniramous. Sixth pleomere elongate. Uropods as oval flaps, margins finely setose. Telson subtriangular, with median keel and 17 pairs of moveable marginal spines.

Remarks.—There is a slight reduction in the size of the first thoracomere, but reconsideration of the original material of Schram and Schram (1974) leaves some question as to whether their first thoracopod is as well developed as those on the other thoracic segments.

The apparent single joint on the antennal protopods may be an artifact of preservation, but oddly coincides with an apparent similar phenomenon on *Praeanaspides praecursor,* which, if it is confirmed, may provide another derived feature to characterize the family.

Genus PRAEANASPIDES Woodward, 1908

Diagnosis.—First thoracomere very reduced. Pleopods biramous. Uropodal exopod with distinct circular diaeresis. Telson rectangular, laterally spinose.

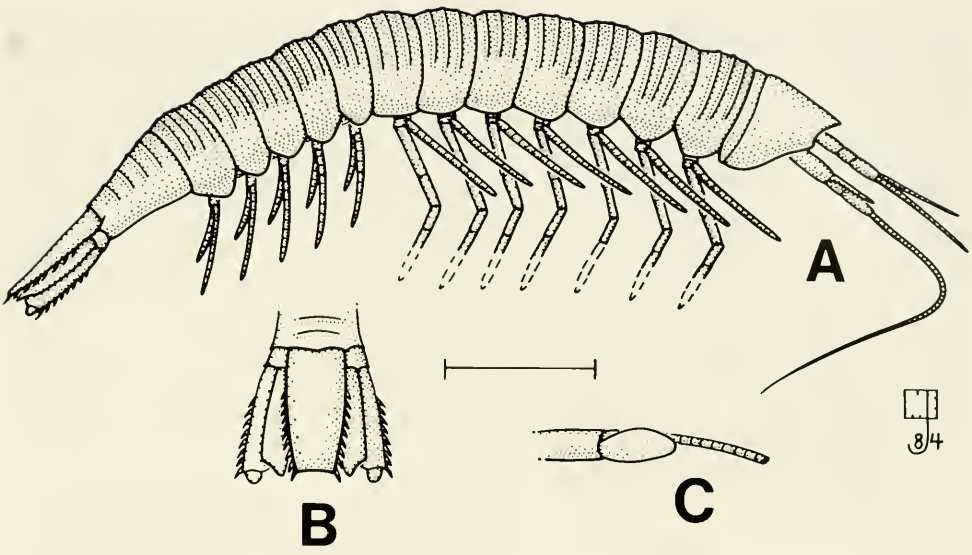


FIGURE 19. A) Reconstruction of *Praeanaspides praecursor,* scale 5 mm (redrawn from Schram 1979*a*); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

Type species.—*Praeanaspides praecursor* Woodward, 1908.

Praeanaspides praecursor Woodward, 1908
Fig. 19

v.*1908 *Praeanaspides praecursor* Woodward, p. 385, figs. 1–5.
v. 1908 *Paleocaris lansboroughi* Peach, p. 55, pl. 8, figs. 8–10.
1911 Paleocaris lansboroughi Peach. Woodward, p. 363.
1927 Paleocaris praecursor (Woodward). Chappuis, p. 605.
1959 Praeanaspides praecursor Woodward. Siewing, p. 10.
1959 Paleocaris praecursor Woodward. Siewing, p. 101.
1932 *Paleocaris praecursor* (Woodward). Calman, p. 537, figs. 1, 2.
1962b Paleocaris praecursor (Woodward). Brooks, p. 249.
1969a Paleocaris praecursor (Woodward). Schram, p. 220, table 1.
1976 Praeanaspides praecursor Woodward. Schram, p. 411.
1979*a Praeanaspides praecursor* Woodward. Schram, p. 112, figs. 54, 55.
1979b Praeanaspides praecursor Woodward. Schram, table 2.
1981 Praeanaspides praecursor Woodward. Schram, p. 131, table 2.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Lectotype.—GSL 30213-14. Shipley Hall, 1¼ miles NW of Ilkestone, Derbyshire, England. Clay Ironstone, top Modiolaris Zone, Middle Coal Measures.

Other locality.—Greenhill, or Woodhill Quarry, near Kilmaurs, Ayrshire; roof of Finnies Main Coal, Middle Coal Measures, Westphalian B.

Description.—Antennules with 3-segment peduncle, middle joint shorter than either proximal or distal unit, flagella relatively short. Antennae with only single segment visible in protopod, oval non-setose scaphocerite, flagellum very long with proximal 2 joints peduncular. Cephalon unornamented, slight rostral projection.

First thoracomere smooth with no ornament, all other segments with 3 or 4 tergal ridges and rounded pleura. First thoracopod apparently reduced (never seen). Second through eighth subequal, ischium and merus longer than carpus and propodus (dactyls not seen). Pleopods with exopod slightly longer than endopods, rami thin. Uropodal exopod lateral margin spinose, endopod subtrapezoidal with its longer margin medial. Telson rectangular but somewhat bilobed terminally, lateral margin with 12–13 pair of moveable spines.

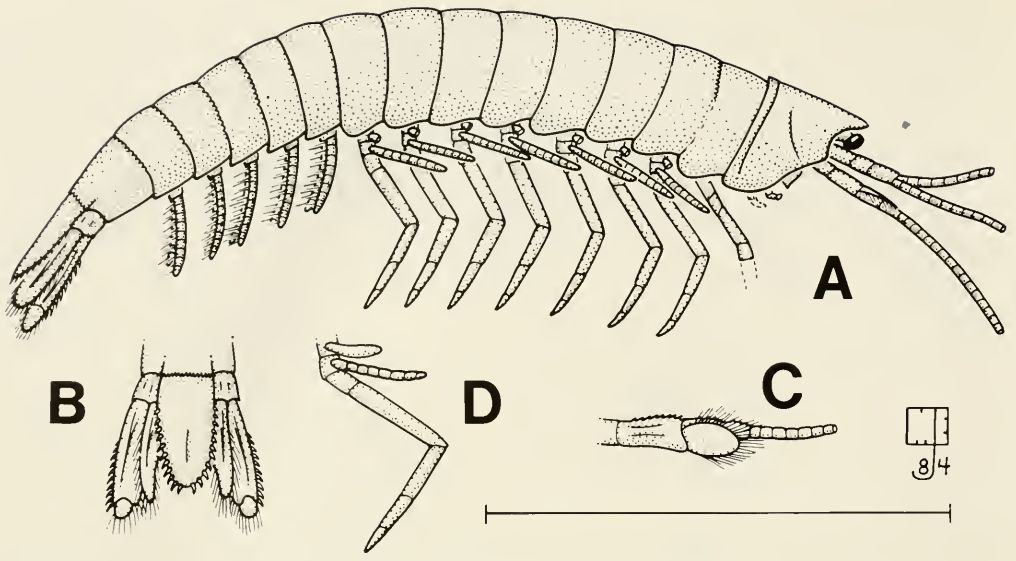


FIGURE 20. A) Reconstruction of *Nectotelson krejcii,* scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna; D) posterior thoracopod. Appendages slightly enlarged.

Remarks.—The apparently single segment antennal protopod is possibly an artifact of preservation, a short proximal segment just may not be observable on known material (however, *see* remarks on *S. spinosus*). The same problem applies to the thoracopodal dactyli; they were probably short and simple, but were simply not preserved on any specimens now available.

Of all the palaeocaridaceans, *P. praecursor* comes closest to resembling the anaspidid anaspidaceans in regard to its very reduced first thoracic segment and in the character of its thoracic and abdominal appendages.

Genus NECTOTELSON Brocchi, 1880

Diagnosis.—All thoracopods (?) and thoracomeres subequal. Pleopods biramous. Uropods spatulate, diaeresis circular. Telson oval and spinose.

Type species.—*Gampsonychus krejcii* Fritsch, 1875.

Nectotelson krejcii (Fritsch) 1875
Fig. 20; Plate 6, fig. H; Plate 7, figs. C–G; Plate 8, fig. A–D

1870 *Gampsonychus* species, Fritsch, p. 34.
1873 *Gampsonychus fimbriatus* Jordan. Feistmantel, p. 593, pl. 18, figs. 9–12.
v.*1875 *Gampsonychus krejcii* Fritsch, p. 104, fig. 265.
v. 1880 *Nectotelson rochei* Brocchi, p. 10, pl. 1.
1885 Gampsonychus fimbriatus (Jordan). Zittel, p. 672 (in part).
1885 *Nectotelson rochei* Brocchi. Zittel, p. 673.
v. 1901 *Gasocaris krejcii* (Fritsch). Fritsch, p. 66, figs. 371–376, pls. 156–158.
1901 Nectotelson rochei Brocchi. Fritsch, p. 74.
1909 *Gasocaris krejcii* (Fritsch). Smith, p. 572, figs. 59–61.
1919 Gasocaris species Fritsch. Pruvost, p. 85.
1919 Nectotelson species Brocchi. Pruvost, p. 85.
1931 Gasocaris species Fritsch. Van Straelen, p. 5.
1959 Gasocaris krejcii (Fritsch). Siewing, p. 5.
1959 Nectotelson rochei Brocchi. Siewing, p. 103.
? 1960 *Eileticus pruvosti* Vandenberghe, p. 690, fig. 2, pl. 17.
1965 Nectotelson species Noodt, p. 82.
1965 Gasocaris species Noodt, p. 82.

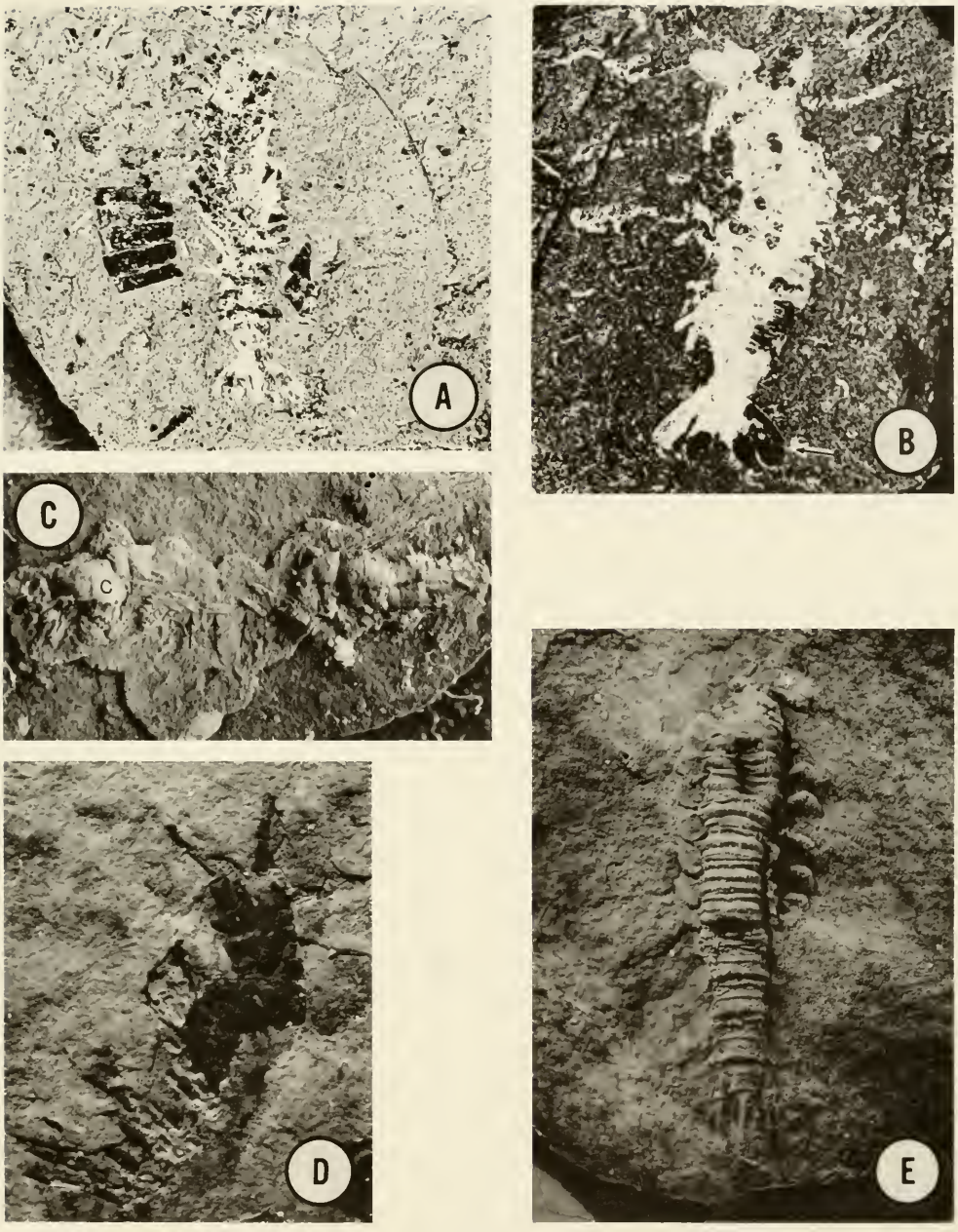


PLATE 8

FIGURES A–D. *Nectotelson krejcii* (Fritsch) 1875; A) lectotype, M 1050, ×4.5; B) Me 40, showing diaeresis on uropodal exopod (arrow), ×5; C) B 7762k, latex peel showing cephalon (c) and thoracopodal epipodites (arrows), ×7; D) B7762j, showing antennules and antennae, and thoracopods, ×7.

FIGURE E. *Pleurocaris annulatus* Calman, 1911; I 13814, latex peel showing thoracic pleura, tergite decoration, and proximal portions of thoracopods, ×6.2.

1969 *Palaeocaris krejcii* (Fritsch). Brooks, p. R355, figs. 170-1b.
1969 *Palaeocaris rochei* (Brocchi). Brooks, p. R355, figs. 170-1c.
1969a Palaeocaris krejcii (Fritsch). Schram, p. 221, table 1.
1969a Palaeocaris rochei (Brocchi). Schram, p. 221, table 1.
1972 *Nectotelson rochei* Brocchi. Secretan, p. 1, 1 fig.

Diagnosis.—Since but a single species is known, the diagnosis of the species is the same as that of the genus.

Lectotype.—M 1050 (Plate 8, fig. A). Humboldt Mine, Nyřan, near Pilsen, Bohemia. Gaskohle, Lower Permian.

Other localities.—Fritsch (1901) also recorded this species from the Gaskohle of the Krimitz Mine and in Třemošná. Brocchi (1880) described the same species under another name from the Lower Permian shales near Autun, central France.

Description.—Cephalon lacks prominent rostral extensions (M 1035, B 7762g, 1), marked by rather deep and prominent mid-dorsal (B 7762b, Plate 7, fig. C) groove parallel to posterior margin which shallows as it extends toward ventral margin (B 7762h). Eye oval, moderate in size (B 7762j, Plate 8, fig. D). Antennular peduncles subequal, 3-segmented middle joint slightly shorter than other two (M 1035, B 7762b, e & j, Plate 8, fig. D. Antennal protopod with short proximal segment and longer distal joint (B 7762e, B 7763b), these with slight longitudinal ridges (Me 40). Scaphocerite short, oval, and setose (Me 40, B 7762e), overlapping 2 proximal-most peduncular joints of flagellum. Antennular and antennal flagella well developed, [of undetermined length because of lack of preservation of distal joints (M 1042, Plate 7, fig. D; B 7762d & j, Plate 7, fig. F)]. Median margin of antennal peduncle marked by row of short denticulae (B 7762e, B 7763k).

Mandible large but not apparently heavily sclerotized or mineralized (B 7763a), with an incisor process (B 7762i, B 7763c). Maxillules and maxillae with small palps, maxillary palp seems to have several segments (B 7763a).

First thoracomere large (B 7762i, Plate 7, fig. E), with fine serrations on posterior margin (B 7763k). Thoracic pleura rounded posteriorly (M 1050, B 77621, and the *N. rochei* holotype). First thoracopod large [but not completely preserved on either the Prague or Paris specimens (e.g., B 7763g)], with moderately long proximal unit (?ischium) followed by short merus, long carpus, and distal to the knee may be at least another short unit. Second through eighth thoracopods (Plate 7, fig. F) subequal; with small epipods (B 7762k, Plate 8, fig. C); stout annulate exopods (M 1042, B 7762d & k); short coxae, bases, and ischia; long meri; and distal to knee progressively shorter carpi, propodi, and dactyli (M 1042 in part, B 7762e, B 7763f & g); posterior margins of endopods with apparently fine setae (B 7762a).

Pleomeres with acute postero-ventral corners (M 7763i); second through sixth pleomeres with finely serrate posterior margins (M 42, M 1033, M 1054, B 7762b). Sixth pleomere almost twice as long as any other segment (M 1054, B 7762f, B 7763b). Pleopods with robust, annulate rami subequal (M 1054, B 7762b & m, B 7763), and setose (M 42).

Uropods longer than telson; protopod short, with 2 faint longitudinal ridges, spatulate rami (B 77621, Plate 6, fig. H), densely setose, and reinforced with sclerotized ribs along most of their lengths (M 1044, M 1054, B 7763h, *N. rochei* type). Exopods laterally spinose (M 1054, B 7762a, B 7763e) diaeresis circular (Me 40, Plate 8, fig. B), segment beyond diaeresis as a narrow oval (M 1033, B 7763d). Telson elongate and oval; ornamented with stout, short, moveable spines set in sockets (M 1033, Plate 7, fig. G; M 1044, M 1054, B 7762b & m, B 7763e).

Remarks.—Both the Bohemian and French specimens are preserved as carbonized films, with varying degrees of pyrite replacement, on a fine-grained thinly-bedded black shale. The pyrite, especially on the Bohemian material, is highly reflective, and makes studying and photographing specimens extremely difficult. In only a few instances were fossils preserved as external molds, and these tend to occur on shale fragments from Autun with a higher content of clay mineral. The matrix in these latter cases was cemented enough to allow one latex peel to be made, but otherwise the shale and fossils are too friable to allow such treatment. In general, the French material is somewhat better preserved in contrast to the Czech specimens.

There are subtle differences between the two suites of specimens, especially as regards the antennal peduncles. That described above generally represents that seen on the better preserved French specimens. The Bohemian material seems to have a somewhat shorter distal segment of the protopod, a somewhat longer scale, and no detectable

TABLE 5. Representative measurements in mm of *Nectotelson krejcii*.

	Cephalon	Thorax	Abdomen	Telson
B 7762a			~3.0	~0.8
B 7762b	1.1	3.8	2.8	0.5
B 7762c				0.8
B 7762d			2.5	0.6
B 7762g	1.2			
B 7762h	1.4			
B 7762i		4.6	3.8	
B 7762l	0.8			
B 7763a		3.2	2.6	
B 7763b				1.0
B 7763c			4.1	
B 7763e			3.3	0.8
B 7763g	~1.3			
B 7763h				1.0
B 7763i			3.4	
B 7763j				1.0
B 7763k	1.4			
B 7763l				0.9
M 1033				0.7
M 1035	~1.3	~5.0		
$\bar{x}$	1.2	4.1	3.2	0.8

medial denticulae. The Czech specimens also have slightly more distinctive spines along the pleomere margins. However, in light of all the other fine and detailed points of agreement between the two series of specimens, and caveats due to vagaries of preservation, I feel that *N. rochei* Brocchi must be synonymized with *N. krejcii* (Fritsch). Nor, in light of the distinctive form of the thoracic exopods and the first thoracomere, can this species be maintained in the genus *Palaeocaris* in the sense of Brooks (1969). Rather, *N. krejcii* is more closely aligned with the Squillitidae.

I found no evidence of any of the sexual dimorphism reported by Fritsch (1901: 70–71). Representative measurements of specimens are given in Table 5.

A vexing problem in this study has been what to do with *Eilecticus pruvosti* Vandenberghe, 1960. The published paper contains no reference as to where the types were deposited; the photographs, while good enough to be intriguing, are not of sufficient quality to facilitate detailed study; and the description of the specimens is too vague to be of any real help. Attempts to find the specimens or locate Dr. Vandenberghe have proved futile. However, certain items in the published description seem to hint that this material may belong within the genus *Nectotelson*. Vandenberghe related that *E. pruvosti* had an abdomen of 7 segments, a thorax of 7 segments, and the first thoracic segment fused with the cephalon. Counts of body segments on the published photographs indicate 14 subequal segments between the head and tailfan. Thus segment count for the abdomen must be wrong, and it seems logical to infer that the abdomen had 6 segments and the thorax 8. The description also makes reference to a deep groove on the cephalon, and spatulate uropodal rami. All these features would seem to correspond to identical characters noted above in *Nectotelson*. Consequently, I choose to assign this species, with a query, to *N. krejcii*. The question mark can be removed only by rediscovery and study of the type, or recollection at the original locality.

E. pruvosti occurs at the top of the Grüner Group, near the Middle and Upper Stephanian boundary. The material came from a borehole in the Saint-Étienne basin, and is associated with the limuline *Pringlia demaistrei*, insects, fish scales, and the plant *Odontopteris pseudoschotheimi*.

Family *uncertain*

Remarks.—The familial taxonomy of the Palaeocaridacea being adopted here is an attempt to establish a more natural system than any used heretofore, and is based on comparative morphology of thoracic and abdominal appendages. Such a system,

however, requires that certain features of the anatomy of these fossils be known before familial assignments can be made. Unfortunately, fossils do not always preserve all the features that one would like to have information about. The fossil syncarids are no exception to this, and as a result there are some Paleozoic taxa that cannot be placed within a family with any degree of certitude, though we can recognize them as distinct and valid genera and species. It was felt here that the issue should not be forced, and that it was preferable to simply recognize the uncertainty and treat these taxa as presently "unassignable." Thoughts as to their affinities can sometimes be offered, but it seems better to patiently await future data which will allow someone to definitively place these problematica.

Genus PLEUROCARIS Calman, 1911*a*

Diagnosis.—Cephalon small, 2 cephalic grooves not joined laterally. Tergites decorated with lateral ridges. Thoracic pleura very large. Telson and uropodal rami styliform.

Type species.—*Pleurocaris annulatus* Calman, 1911*a*.

Pleurocaris annulatus Calman, 1911*a*
Fig. 21; Plate 8, fig. E

? *1881 Palaeocaris burnetti* Woodward, p. 534, pl. 14, figs. 3a, 3b.
v.*1911*a Pleurocaris annulatus* Calman, p. 156, fig. 1.
v. 1911*b Pleurocaris annulatus* Calman. Calman, p. 494, fig. 5.
. 1912 *Eileticus* cf. *aequalis* Scudder. Pruvost, p. 66, pl. 2, figs. 6, 7.
1915 Pleurocaris annulatus Calman. Chappuis, p. 173.
1919 *Pleurocaris annulatus* Calman. Pruvost, p. 86, fig. 21, 22; pl. 25, fig. 11.
. 1919 *Eileticus* cf. *aequalis* Scudder. Pruvost, p. 89, fig. 23; pl. 25, fig. 12.
1922 Eileticus aequalis Scudder. Pruvost, p. 149.
1923 Pleurocaris annulatus. Calman. Pruvost, p. 149.
1927 Pleurocaris annularis Calman. Chappuis, p. 605.
1959 Palaeocaris burnetti Woodward. Siewing, p. 101.
1959 Pleurocaris annulatus Calman. Siewing, p. 103.
1962a Pleurocaris annulatus Calman. Brooks, p. 236.
1965 Pleurocaris species. Noodt, p. 83.
1969 *Pleurocaris annulatus* Calman. Brooks, p. 355, fig. 169-5, 172.
1969a Pleurocaris annulatus Calman. Schram, p. 220, table 1.
? *1969a Palaeocaris burnetti* Woodward. Schram, p. 220, table 1.
1976 Pleurocaris annulatus Calman. Schram, p. 411.
1979*a Pleurocaris annulatus* Calman. Schram, p. 103, figs. 48, 49.
1979b Pleurocaris annulatus Calman. Schram, p. 167, table 2.
1981*a Pleurocaris annulatus* Calman. Schram, p. 131, text-fig. 5f; table 2.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Holotype.—In 29008. Clay Croft mine, Coseley, near Dudley, Worcestershire, England. Ten foot Ironstone Measures, Lower Similis–Pulchra Zone, Middle Coal Measures, Upper Carboniferous.

Other localities.—Pit no. 9, near Lens, Belgium; Black shale of the Insect beds, beneath the "veine Girard," Edouard Group, Westphalian C. Pit no. 4, Vicoigne Mines, France; Black shale, top of the "veine du Nord," Olympé Group, Westphalian A.

Descriptions.—Cephalon short, rostrum small. Stalked compound, eyes small and rounded. Details of antennules and antennae uncertain.

First thoracomere short, about half the length of any other. All thoracomeres with 2 laterally directed ridges on tergites; pleura very large, rounded, set off from tergites as lappets. Second through eighth thoracopods with well-developed endopods, meri long, carpi short (other joints indeterminable).

Pleomeres decorated dorsally with lateral ridges as thoracomeres, pleura decrease in development posteriorly. Telson styliform, margins with 5 pair moveable spines. Pleopods possibly flap-like (I 14449). Uropods as blades; exopod straight, serrated laterally and less conspicuously so medially; endopod curved mediad, lateral margin faintly spined, medial margin distinctly so.

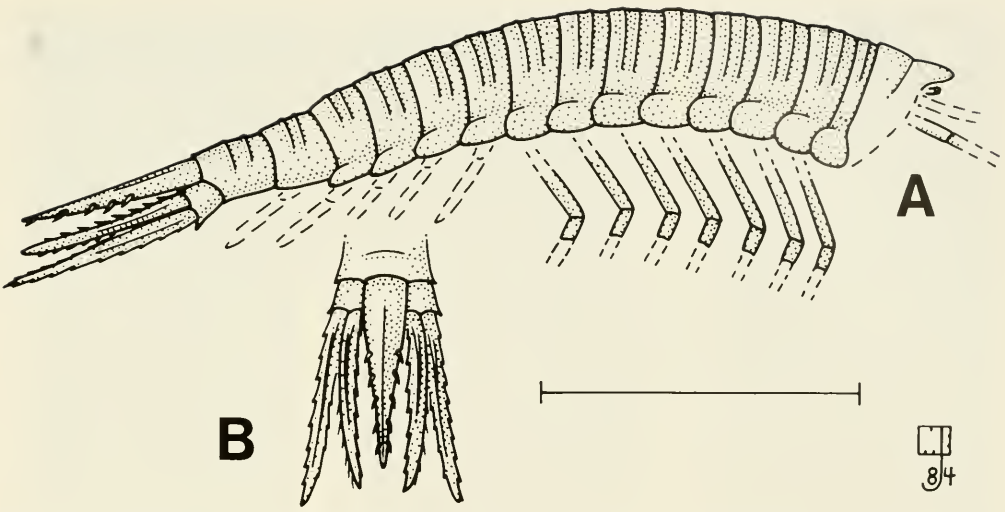


FIGURE 21. A) Reconstruction of *Pleurocaris annulatus*, (modified from Calman 1911*a*; and Schram 1979*a*), scale 5 mm; B) tailfan to same scale as body.

Remarks. One specimen, In 14449, appears to have some poorly preserved proximal portions of the pleopods. These appear to be flap-like. However, they are of such quality as to be almost impossible to photograph. This was not noticed in the original study of Schram (1979*a*). Though the few British specimens known of this species (Schram 1979*a*:121) are for the most part moderately well preserved, our knowledge of this taxon suffers because there are so few examples of it. All continental European material attributable to this species has been lost. However, examples of this species on the continent have apparently never been common, just as in Britain.

Confusion in the identification of specimens of this species with *Acanthotelson stimpsoni* arises from the somewhat similar syliform telson and uropods. However, the short cephalon, subequal second through eighth thoracomeres, large thoracic pleura, and tergal decoration clearly justify a separate generic status for this species (Plate 8, fig. E). However, exact familial affinities must remain uncertain until such time as the structure of the thoracic exopods, distal joints of the endopods, and pleopods can be ascertained. The general form of the tailfan noted here, as well as a supposed analogue correspondence to *A. stimpsoni* in the Carboniferous brackish water habitat community (Schram 1981*a*) may suggest that *P. annulatus* could be eventually assigned to the acanthotelsonids.

Pruvost (1912, 1919) described 2 syncarid specimens which he variously referred to *Eileticus* cf. *aequalis* and/or *Pleurocaris annulatus*. The specimens were deposited in the museum at the University of Lille, but are now lost. The published descriptions and illustrations of these specimens, combined with Pruvost's own stated reservations on what he called *E.* cf. *aequalis*, indicate these were indeed examples of *P. annulatus*.

Genus WILLIAMOCALMANIA new genus

Diagnosis.—First thoracomere markedly reduced, second thoracomere longer than first but less than any other thoracomeres. Thorax shorter than abdomen, ratio about 0.9:1. Telson elongate, subtriangular, distal end rounded. Uropodal rami oval, somewhat longer than telson.

Type species.—*Palaeocaris vandergrachti* Pruvost, 1922.

Etymology.—Named in honor of W. T. Calman, among whose many accomplishments was his expertise on fossil and recent syncarids.

Remarks.—The distinctive pattern of reduction of the anterior thoracomeres, the unique thorax-abdomen ratio, and the characteristic tailfan clearly separate this species

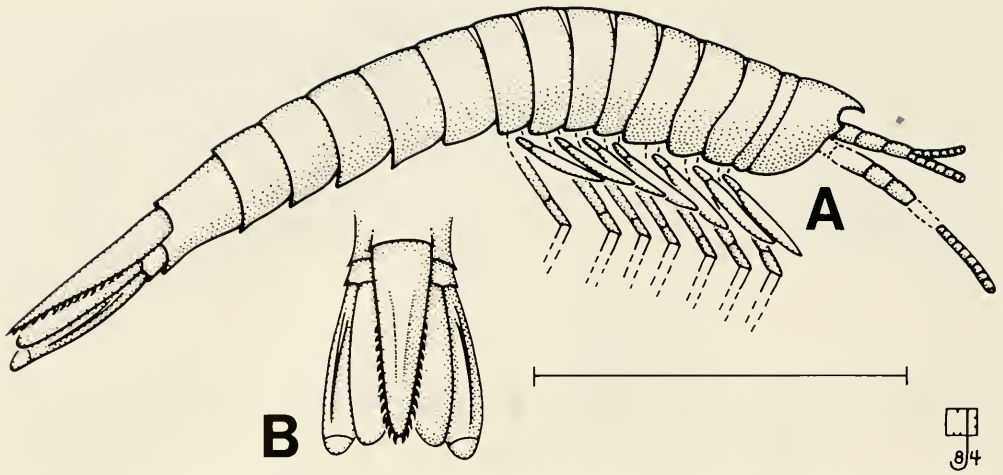


FIGURE 22. A) Reconstruction of *Williamocalmania vandergrachti*, scale 5 mm; B) tailfan to same scale as body.

from those herein included in the newly redefined genus *Palaeocaris*. Consequently, a separate generic designation is necessary for this taxon. Though obviously distinct from *Palaeocaris* or any other known fossil syncarid, the lack of sufficient information about body appendages dictates an uncertain family affinity for this species.

Williamocalmania vandergrachti (Pruvost) 1922
Fig. 22; Plate 9, figs. A–C

v*1922 *Palaeocaris vandergrachti* Pruvost, p. 147, fig. 1.
1927 Palaeocaris vandergrachti Pruvost. Chappuis, p. 605.
1930 *Palaeocaris vandergrachti* Pruvost. Pruvost, p. 181, fig. 5, pl. 8.
1959 Palaeocaris vandergrachti Pruvost. Siewing, p. 101.
1969a Palaeocaris vandergrachti Pruvost. Schram, p. 220, table 1.

Diagnosis.—Since but one species is known, the diagnosis of the species is the same as that of the genus.

Lectotype.—NB 7183 Ech. no. 1 (see Pruvost 1930, plate 8, fig. 1a). Woensdrecht borehole (1164–1167 m), The Netherlands; Chokier Ampélite, Lower Namurian.

Description.—Body moderate to large in size. Antennular peduncle large, with 3 subequal segments. Antennal peduncles large, scaphocerite appears large and ovoid, 2 (or 3) proximal-most segments of flagellum peduncular and very large. Cephalon with rostrum, prominent optic notch.

First thoracomere reduced and closely associated with cephalon, second thoracomere shorter than posterior thoracomeres but larger than first, all other thoracic and anterior abdominal segments subequal. Pleura somewhat subtriangular, attenuated along anterior margin (Plate 9, fig. C), with slight marginal furrows. Thoracopods apparently equally developed, exopods possibly flap-like (Plate 9, fig. A). Thorax somewhat shorter in length than abdomen.

Sixth pleomere elongate. Telson long, subtriangular with distal end rounded, margins with stout spinose setae (Plate 9, figs. B & C). Uropodal rami oval; exopod reinforced proximally with medial rib, with slightly curved diaeresis, somewhat longer than endopod.

Remarks.—The later treatment by Pruvost (1930) of this species is superior in most respects to the original description (Pruvost 1922), especially in regards to the plate figures which illustrate all 4 of the available specimens. Pruvost, however, claimed in his original description to have studied 12 specimens. The only substantially complete

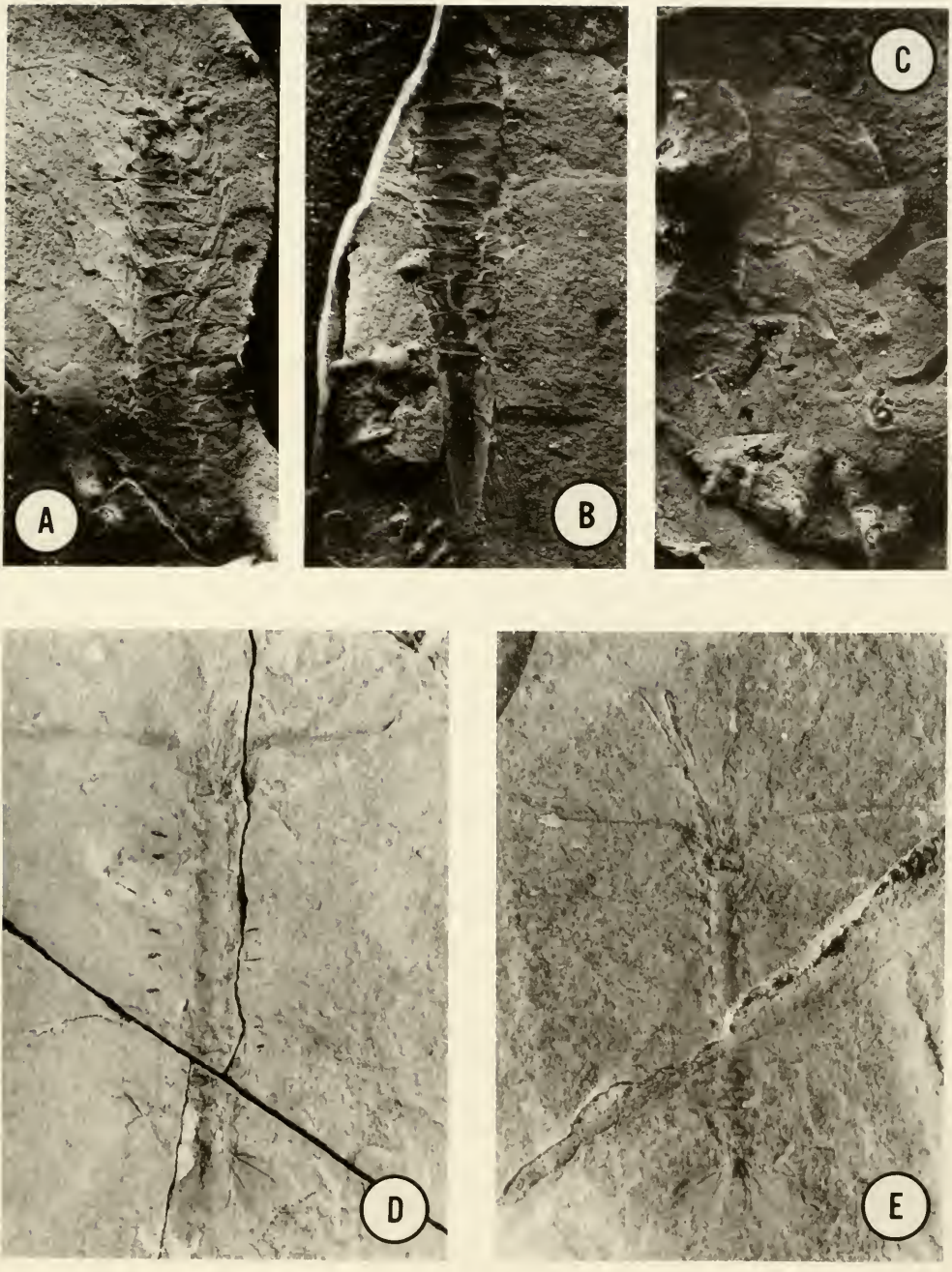


PLATE 9

FIGURES A–C. *Williamocalmania vandergrachti* (Pruvost) 1922; A) NB 7183 Ech. no. 3, note reduced first thoracomere (arrow), ×7.6; B) NB 7183 Ech. no. 4, showing long, subtriangular telson, ×7; C) NB 7183 Ech. no. 2, showing somewhat acute abdominal pleura, ×7.8.

FIGURES D & E. *Palaeorchestia parallela* (Fritsch) 1876, part and counterpart of lectotype, CGH 593, showing the characteristic parallel-sided, distally circular telson; D) under water ×3.6; E) ×2.9.

TABLE 6. Measurements of lengths in mm of *Williamocalmania vandergrachti*. * Lectotype.

	Cephalon	Thorax	Abdomen	A_6	Telson
NB 7183 Ech. 1	~1.2	4.7	5.6	1.3	2.3
2			6.4	1.2	* 2.3
3	0.8	4.5			
4			4.0	0.9	2.2

specimen now available, NP 7183 Ech. no. 1, clearly is the basis for the 1922 and 1930 figure drawings, and thus designated here as the lectotype. Some measurements are provided in Table 6.

BROOKSYNCARIS new genus

Diagnosis.—First thoracomere only slightly reduced, sixth through eighth thoracomeres slightly larger than second through fifth. Thoracomeres each with 2 transverse grooves.

Type species.—*Palaeocaris canadensis* Brooks, 1962*b*.

Etymology.—Named in honor of H. K. Brooks.

Brooksyncaris canadensis (Brooks), 1962*b*

Fig. 23; Plate 10, fig. A

v*1962*b Palaeocaris canadensis* Brooks, p. 248; pl. 15, figs. 1, 2.
1969a Palaeocaris canadensis Brooks. Schram, p. 220, table 1.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Holotype.—MCZ 5435 (Plate 10, fig. A); Confluence of Diligent and Ramshead Rivers, south of Diligent River, Cumberland County, Nova Scotia; Riversdale Group, Westphalian A.

Description.—Cephalon short (cephalon to thorax ratio 1:5.4); prominent cephalic groove; small postcephalic groove extending in arc dorsad from posterior margin.

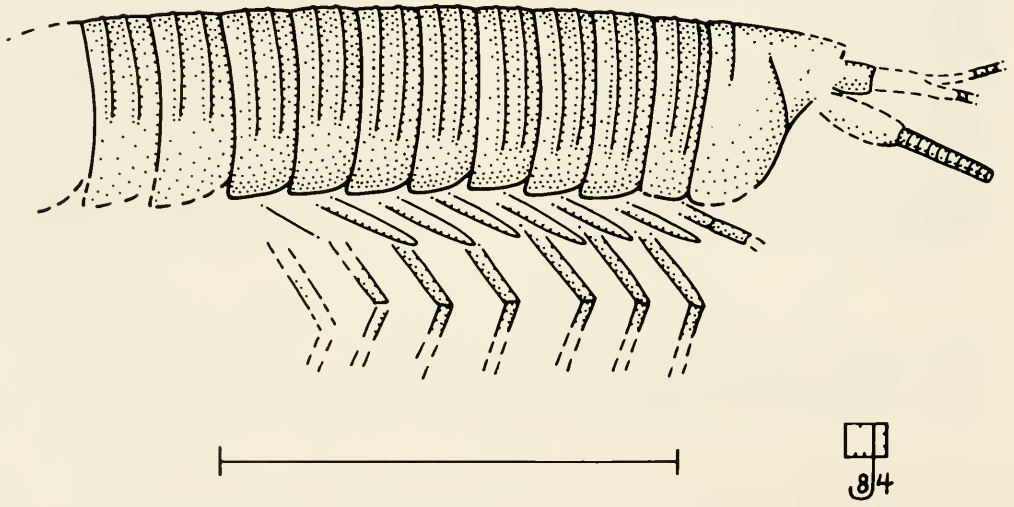


FIGURE 23. Diagrammatic rendition of what is currently known about the form of *Brooksyncaris canadensis*, scale 5 mm.

Antennual and antennal peduncles well developed [too poorly preserved to discern details].

First thoracomere not much reduced. Second through eighth thoracopods ambulatory, with large(?) epipodites.

Remarks.—The specimens discussed by Copeland (1957*a, b*) and referred by Brooks (1962*b*) to this species have been reexamined by me. I concur with Copeland's original treatment of that material and refer those specimens to *Palaeocaris* cf. *typus*. Thus, the only material that is referable to *B. canadensis* is the holotype.

Brooks (1962*b*) described the thoracopods of this species as bearing epipodites. I have concurred with this for the time being, but it is difficult to clearly discern whether these structures are epipodites or flap-like exopods. These features are located very close to the base of the limbs, and I would also assume that the exopods probably would have been as poorly preserved as the endopods. However, the question remains open.

The new genus is required because this species obviously does not belong in *Palaeocaris* as now understood, the latter taxon being characterized in part by the extreme reduction of the first thoracomere. However, none of the pertinent features of the thoracopods, abdomen, pleopods, or tailfan are preserved on the holotype that would allow us to place this species in any of the known genera of palaeocaridaceans, let alone family. Thus the establishment of a separate genus seems prudent.

Genus PALAEORCHESTIA Zittel, 1885

Diagnosis.—Antennular peduncles smaller than those of antennae. Telson distinctly rectangular.

Type species.—*Gampsonychus parallelus* Fritsch, 1876.

Remarks.—Determining the proper name for this genus poses a classic problem in untying the twisted strands of available names among Paleozoic syncarids. Jordan (1847) originally described *Gampsonyx fimbriatus,* unaware of the fact that the name of this genus was preoccupied in a bird, *Gampsonyx swainsoni* Vigors, 1825. Bronn (1850) did detect the synonymy and suggested the name *Uronectes* be applied to *G. fimbriatus*; while Burmeister (1855) independently caught the same synonymy and, unaware of Bronn's work, suggested the use of the name *Gampsonychus* for *G. fimbriatus.* Subsequent authors, until Chappuis (1927), ignored Bronn and used either *Gampsonyx* (and thus also ignoring the synonym) or *Gampsonychus.*

In this context Fritsch (1876) described a new species *Gampsonychus parallelus* and allied it to *G. fimbriatus.* Zittel (1885) recognized the distinctive generic status of this species from *fimbriatus* and erected a new combination *Palaeorchestia parallela.* Brooks (1969) seemingly concurred with the Zittel distinction of *P. parallelus* from what by then was known as *U. fimbriatus,* but implied that the proper generic assignment of the species was supposedly with *Palaeocaris* when he synonymized *Palaeoorchestia* (*lapsus calumni*), along with other syncarid genera, with *Palaeocaris.* Brooks was mistaken, since the taxa in question are distinctly different. One might be technically entitled to return to the use of *Gamsonychus,* since the use of *Gampsonychus* in Fritsch (1876) is not affected by any subjective synonymy in Burmeister (1855). However, to do so would be to: 1) return to the 19th and early 20th century confusion over the use of *Gamsonyx-Gampsonychus,* 2) minimize the importance of Zittel's initial recognition of the separate generic status of the type species, and 3) overlook Brooks' implicit acceptance of Zittel's work. For these reasons, I think the decisions of Brooks *and* Zittel should prevail and the name *Palaeorchestia* be used.

Palaeorchestia parallela (Fritsch), 1876
Fig. 24; Plate 9, figs. D & E

1859 cf. *Gampsonychus fimbriatus.* Krejci, p. 79.
v*1876 *Gampsonychus parallelus* Fritsch, p. 4, pl. 3 fig. 1, pl. 4.
1885 *Palaeorchestia parallela* (Fritsch). Zittel, p. 673, fig. 858.

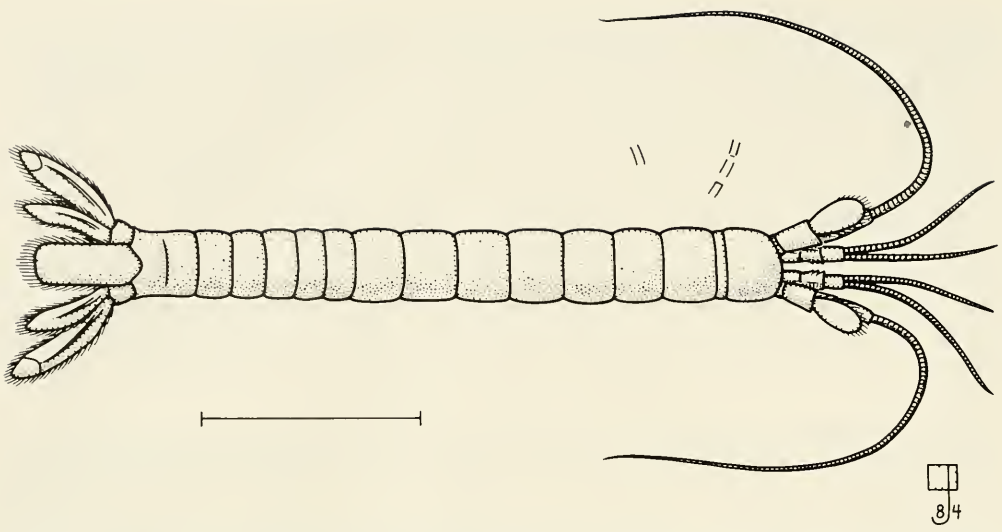


FIGURE 24. Dorsal reconstruction of what is currently known about the form of *Palaeorchestia parallela*, scale 5 mm.

1901 Palaeorchestia parallela (Fritsch). Fritsch, p. 73.
1916 Palaeorchestia parallela (Fritsch). Vanhöffen, p. 146, fig. 11.
1959 Palaeorchestia parallela (Fritsch). Siewing, p. 103.
1965 Palaeorchestia species Noodt, p. 82.
1969 Palaeocaris parallela (Fritsch). Brooks, p. R355.

Diagnosis.—Since but one species is known, the diagnosis of the species is the same as that of the genus.

Lectotype.—CGH 593 (Plate 9, figs. D & E), from Lisek, northwest of Beraun, Bohemia, Czechoslovakia. Rodnitz Horizon, Coal Measures, Lower Permian. [The stratigraphic horizon is somewhat vague in the literature. One specimen in the British Museum (Natural History), In 35327, which resembles the preservation seen in the Czech types, is marked "Carboniferous, Nirzan, near Pilsen, Bohemia—Old Colln." seems to indicate the type Lower Permian area in Czechoslovakia.]

Description.—Body moderate in size. Antennular peduncle with 3 subequal segments, medial margin of second segment spinose, flagella well developed. Antennal protopod with short proximal segment, scaphocerite large and setose, basal joints of flagellum peduncular with distal segment twice as long as proximal. No rostrum.

First thoracomere somewhat shorter than any other body segment. Thorax length more than one and one-half times that of abdomen.

Sixth pleomere very long, with faint lateral groove about mid-length. Telson long, subrectangular, marginally setose. Uropodal rami spatulate, with strong median ribs, margins finely setose, exopod larger than endopod, endopod equal to or shorter than telson, exopod with circular diaeresis.

Remarks.—Fritsch (1876, 1901) referred to only one specimen. CGH 593 is obviously the basis of Plate 4 in his 1876 paper, and is thus designated the lectotype here. However, one additional specimen, CGH 592, is in the collections of the National Museum in Prague. It confirms the form of the head and antennae noted on the type, and clearly reveals the slight reduction in size of the first thoracomere.

Aside from the antennules, antennae, and uropods, virtually nothing is known concerning any of the other appendages. CGH 593 preserves some remnants of anterior thoracopods. Both specimens are preserved in dorsal view in a brownish-gray mudstone, and details on the thorax and anterior abdomen are almost totally lacking. The additional specimen in the British Museum, In 35327, contributes nothing towards understanding this species.

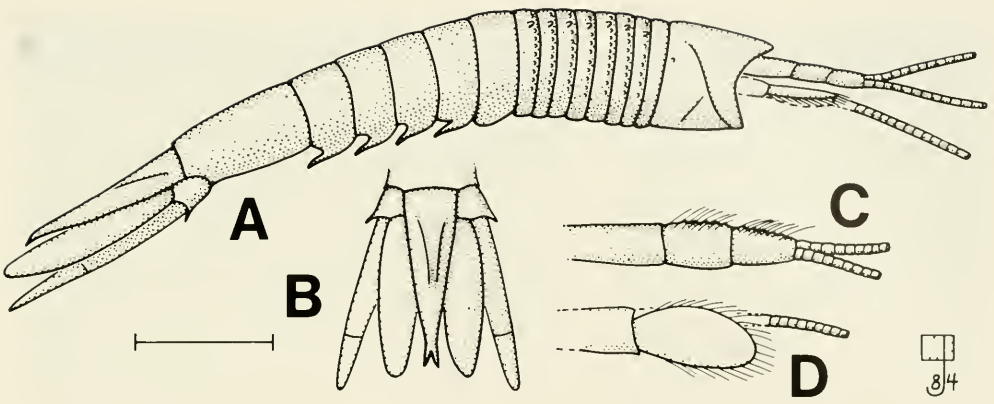


FIGURE 25. A) Partial reconstruction of *Clarkecaris brasilicus,* scale 5 mm; B) tailfan to same scale as body; dorsal views of C) right antennule and D) antenna slightly enlarged.

Genus CLARKECARIS Mezzalira, 1952

Diagnosis.—Cephalon with well-developed groove. Eight free thoracic segments short. Abdominal segments long, especially the sixth, pleura styliform. Telson subtriangular, with a narrow bifid terminus.

Type species.—*Gampsonyx brasilicus* Clarke, 1920.

Remarks.—The higher taxonomic placement of this species has been rather peripatetic. It was originally placed among the "gamsonychids," but when Mezzalira (1952) recognized the separate generic status of this creature he assigned it to the Uronectidae. However, Mezzalira's understanding of "uronectids" was not that of Brooks (1962*a*). The latter placed *Clarkecaris* in its own family within the anaspidaceans; though later (Brooks 1969) he reassigned it to the stygocaridaceans, still within its own family. Stygocaridines have since been recognized as a group within the Anaspidacea. However, reexamination of the types and an additional specimen studied and illustrated by Brooks (1962*a,* 1969), as well as information from new material from Brazil (Dr. Irajá Domiani Pinto, *pers. comm.*), reveals that there are 8 free subequal thoracomeres, placing this species within the Palaeocaridacea.

Clarkecaris brasilicus (Clarke) 1920
Fig. 25; Plate 10, figs. B–D

v.**1920 Gampsonyx brasilicus.* Clarke, p. 137, pl. 3, figs. 9, 10.
1927 Uronectes brasilicus (Clarke). Chappuis, p. 605.
1931 Uronectes braziliensis (Clarke). Van Straelen, p. 18.
1946 Gampsonyx brasilicus Clarke. Mezzlira, p. 118, figs. 9, 10.
1946 Uronectes brasilicus (Clarke). Mezzalira, p. 118.
1948 Uronectes brasilicus (Clarke). Mezzalira, p. 250.
1952 *Clarkecaris brasilicus* (Clarke). Mezzalira, p. 46, pl. 3.
1954 Clarkecaris brasilicus (Clarke). Mezzalira, p. 168.
1959 Gampsonyx brasilicus Clarke. Siewing, p. 100.
v. 1962*a Clarkecaris brasilicus* (Clarke). Brooks, p. 231; Fig. 2b; pl. 5, fig. 2.
1962b Clarkecaris brasilicus (Clarke). Brooks, p. 274.
1969 *Clarkecaris brasilicus* (Clarke). Brooks, p. R358, figs. 169-3, 174-2.
1969 Clarkecaris brasilicus (Clarke). Schram, p. 221, table 1.
1971 *Clarkecaris brasilicus* (Clarke). Mezzalira, p. 319, pl. 1, fig. 1, pl. 3, figs. 1–6.
1977 Clarkecaris brasilicus (Clarke). Schram, p. 370.
1978 *Clarkecaris brasilicus* (Clarke). Brito and de Quadros, p. 417, fig. 3.
1979 Clarkecaris brasilicus (Clarke). Schram, p. 170.
1981 Clarkecaris brasilicus (Clarke). Schram, p. 130.

Lectotype.—NYSM 9738 (Plate 10, fig. D); near Guare'í, São Paulo, Brazil; Irati Formation, Permian.

Other localities.—Innumerable localities for this species are known in the states of Panamá and São Paulo, in Brazil. These are summarized in Mezzalira (1948, 1954) and Brito and de Quadros (1978).

Description.—Cephalon with well-marked groove (Plate 10, fig. C). Antennules large, with well-developed peduncles medially serrate and setose. Antennae with large, oval, setose scaphocerite. Flagella well developed.

Thoracomeres short, subequal in length, anterior margins marked with row of papillae, pleura apparently rounded.

Abdominal segments long (Plate 10, fig. D), sixth longer than any others. Pleura various: first rounded, second through fifth with styliform posteriorly directed processes. Uropodal protopod with lateral styliform processes; exopod long and thin (possibly a straight diaeresis); endopod diaphanous, long, and oval. Telson shorter than uropod rami, narrow, subtriangular, terminus developed as bifed process (Plate 10, fig. B).

Remarks.—The description here is based on observations derived from study of the types (NYSM 9738, 9739), USNM 112766, and the published figure in Brito and de Quadros (1978). Considerable more information should become available, however, as the collections available to Dr. Damiani Pinto of the Instituto de Geosciências, Porto Alegre, Brazil, are eventually studied and described. These should allow a definitive placement of *C. brasilicus* within the palaeocaridacean families.

Suborder ANASPIDACEA Calman, 1904
Infraorder ANASPIDINEA Calman, 1904
Family ANASPIDIDAE Thompson, 1894
Genus ANASPIDITES Brooks, 1962*a*

Diagnosis.—Rostrum broad. Thoracomeres relatively short compared to anterior pleomeres. Telson subtriangular, distally pointed.

Type species.—*Anaspides antiquus* Chilton, 1929.

Remarks.—The initial observations on this taxon (Chilton 1929, Brooks 1962*a*) were largely based on one incompletely preserved specimen. A search in 1980 of the reserve collections of the Australian Museum uncovered one additional specimen (F 25226), which preserves the abdomen and parts of the tailfan. In addition, two specimens were found in the British Museum (Natural History). One of these (In 46114) is the finest example of this species known, revealing considerable details about appendage anatomy. The other (In 46056) is of the uropodal exopods. Consequently, a redescription of the species and new reconstruction are presented here.

Anaspidites antiquus (Chilton) 1929
Fig. 26; Plate 10, figs. E & F

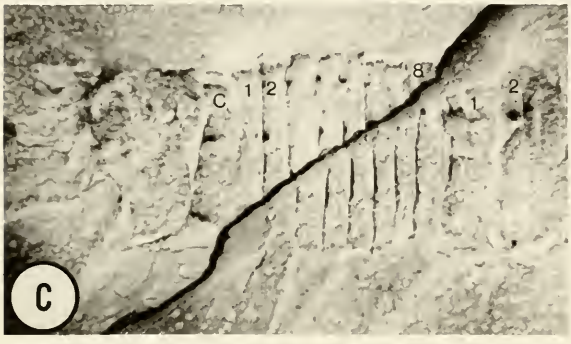
v.*1929 *Anaspides? antiquus* Chilton, p. 366, pl. 30.
1962*a Anaspidites antiquus* (Chilton). Brooks, p. 234; pl. 5, fig. 1; figs. 1 & 2c.
1962b Anaspidites. species Brooks. Brooks, pp. 267, 274.
1969 *Anaspidites antiquus* (Chilton). Brooks, p. R356, figs. 169-4, 174-1.
1982 Anaspidites antiquus (Chilton). Schram, p. 122.

Diagnosis.—Since there is but one species known, the diagnosis of the species is the same as that of the genus.

Holotype.—US 7903. Brookvale Brick Quarry, New South Wales. Hawksbury Sandstone, Triassic.

Description.—Cephalon with broad rostrum, prominent cervical groove. Antennular peduncles large, with 3 subequal segments, flagella well developed [but length indeterminate because of lack of preservation]. Antennal peduncles with 4 (?) segments (US 7903). Mandibles large, massive.

Thoracomeres somewhat shortened, almost one-half the length of anterior pleomeres (US 7903, In 46114). Pleura somewhat rounded (In 46114). Thoracopods (Plate 10, fig. F) with short coxae, bases, and ischia, long meri (In 46114); beyond knee, long



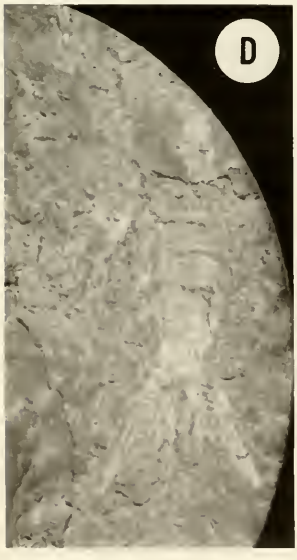


PLATE 10

FIGURE A. *Brooksyncaris canadensis* (Brooks) 1962, closeup of anterior end with cephalon (c) and first 4 thoracomeres (numbered), ×8.9.

FIGURES B–D. *Clarkecaris brasilicus* (Clark), 1920; B) paralectotype, NYSM 9739, showing telson with pointed tip (t) and styliform uropods (u), ×7; C) USNM 112766, closeup of anterior end, note cephalon, size of thoracomeres (numbered) and anterior pleomeres (numbered), ×4.5; D) NYSM 9738, lectotype, with posterior thorax and abdomen, ×2.8.

FIGURES E & F. *Anaspidites antiquus* (Chilton) 1929; E) F 25226, with abdomen and telson, ×1.8; F) In 46114, whole body, note annulate pleopods (arrows), ×1.6.

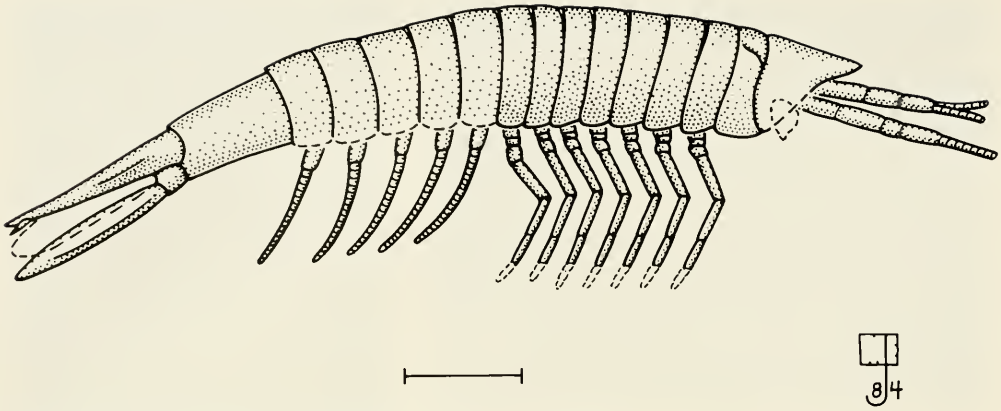


FIGURE 26. Reconstruction of *Anaspidites antiquus*, scale 5 mm.

carpi and propodi (US 7903, In 46114), dactyli incompletely preserved (In 46114). Neither thoracic epipodites nor exopods preserved.

Pleomeres undecorated. Sixth pleomere length twice that of any anterior to it. Pleopods long, uniramous, annulate (In 46114, Plate 10, fig. F), protopods well developed. Telson long, subtriangular, distally pointed (F 25226, Plate 10, fig. E) (perhaps some faint indication that terminus possibly flanked by set of small furcae). Uropodal protopod simple, well developed (In 46056, In 46114). Exopod blade-like (F 25226, In 46114), reinforced with thick struts along lateral and medial margins (In 46056).

Remarks.—Brooks (1962*a*) interpreted a 2-segment protopod on the antennae (with only the distal segment visible), a straight-edged scaphocerite, and the 3 most proximal joints of the flagellum as peduncular. I found no evidence for an antennal scale on either US 7903 or In 46114. Brooks also felt that the thoracopods were widely spaced, on opposite ends of well-developed thoracic sternites. Close examination of US 7903 indicates that the supposed foramina of the thoracopods are more likely preservational anomalies of the cuticular wrinkles or possibly ridges on the anterior thoracomeres. Finally, the pleopod that Brooks noted is in fact part of a posterior thoracopod.

Although the general mode of preservation of these fossils obscures much of the detail, enough can be discerned to be reasonably certain *A. antiquus* is an anaspid. The body is large and well developed, but the first thoracomere is fused into the cephalon, and the rami of the pleopods are clearly uniramous and annulate. However, the narrow thoracic somites and styliform telson clearly separate this Triassic species from the living forms found today in Tasmania. Unfortunately, the diagnostic features of the mouthparts are not visible on any of the available material of *Anaspidites,* and as a result exact assurance as to family affinities within the Anaspidacea must remain uncertain.

ACKNOWLEDGMENTS

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Geologische Dienst, Heerlen; and R. Wilson, Institute of Geological Sciences, Edinburgh. Photographic and technical assistance was rendered by Messrs. B. R. Burnett, R. M. Chandler, and T. A. Deméré, San Diego Museum; and the reconstructions were drawn by Mr. M. J. Emerson.

Literature Cited

Berry, C. T. 1939. A summary of the fossil Crustacea of the order Stomatopoda and a description of a new species from Angola. American Midland Naturalist 21:461–471.

Boy, J. A. 1972. Palökologischer Vergleisch zweier berühmter Fossillagenstätten des deutschen Rotliegenden (Unterperm, Saar-Nahe-Gebiet). Notizenblatt des hessischen Landesamtes für Bodenforschung 100:46–59.

Brito, I. M., and L. P. de Quadros. 1978. Ocorrência inédita de *Clarkecaris brazilicus* no Permiano do Estado de Paraná. Anais Acadamia Brasileira Ciências 50:417–421.

Brocchi, P. 1880. Note sur un Crustacé fossile recueilli dans les schistes d'Autun. Bulletin de la Société Géologique de France (3)8:5–10, pl. 1.

Bronn, H. G. 1848. Ueber *Gampsonyx fimbriatus* Jordan. Neues Jahrbuch für Minerologie, Geologie, und Paläontologie 1848:125–126.

———. 1850. Ueber *Gampsonyx fimbriatus* Jordan aus der Steinkohlenformation von Saarbrücken und vom Murg-Thal. Neues Jahrbuch für Minerologie, Geologie, und Paläontologie 1850:575–583.

Brooks, H. K. 1962*a*. On the fossil Anaspidacea, with a revision of the classification of the Syncarida. Crustaceana 4:229–242.

———. 1962*b*. The Paleozoic Eumalacostraca of North America. Bulletins of American Paleontology 44:163–338.

———. 1969. Syncarida, pp. 345–359 *in* R. C. Moore (ed.). Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Vol. 1. Geological Society of America and University of Kansas, Lawrence.

Burmeister, H. 1855. Ueber *Gampsonychus fimbriatus* Jordan. Abhandlungen der naturforshenden Gesellschaft zu Halle 2:191–200, pl. 10, figs. 12–14.

Calman, W. T. 1896. On the genus *Anaspides* and its affinities with certain fossil Crustacea. Transactions of the Royal Society of Edinburgh 38:787–802.

———. 1902. *Uronectes* and *Anaspides*, a reply to Prof. Anton Fritsch. Zoologisches Anzieger 25:65–66.

———. 1904. On the classification of the Malacostraca. Annals and Magazine of Natural History 13(7):144–158.

———. 1911*a*. On *Pleurocaris*, a new crustacean from the English Coal Measures. Geological Magazine 8(5):156–160.

———. 1911*b*. On some Crustacea of the division of Syncarida from the English Coal Measures. Geological Magazine 8(5):488–495.

———. 1932. Notes on *Palaeocaris praecursor*, a fossil crustacean of the division Syncarida. Annals and Magazine of Natural History 10(10): 537–541.

Chappuis, P. A. 1915. *Bathynella natans* und ihre Stellung im System. Zoologisches Jahrbuch 40: 147–176.

———. 1927. Anaspidacea, pp. 593–606 *in* W. Kukenthal and T. Krumbach (eds.). Handbuch der Zoologie III(1). de Gruyter, Berlin.

Charig, A. J. 1982. Systematics in biology: a fundamental companion of some major schools of thought, pp. 363–440 *in* K. A. Joysey and A. E. Friday (eds.). Problems of Phylogenetic Reconstruction. Academic Press, London.

Chilton, C. 1929. Note on a fossil shrimp from Hawkesbury sandstones. Journal of the Royal Society of New South Wales 62:366–368.

Clarke, J. M. 1920. Crustacea of the Permian of São Paulo, Brazil. Bulletin of the New York State Museum 219/220:135–137.

Cockerell, T. D. A. 1916. The uropods of *Acanthotelson stimpsoni*. Journal of the Washington Academy Science 6:234–236.

Copeland, M. J. 1957*a*. The Carboniferous genera *Palaeocaris* and *Euproops* in the Canadian Maritime Provinces. Journal of Paleontology 31:595–599.

———. 1957*b*. The arthropod fauna of the Upper Carboniferous rocks of the Maritime Provinces. Memoirs of the Geological Survey of Canada 286:1–110.

Dahl, E. 1983. Malacostracan phylogeny and evolution. Crustacean Issues 1:189–212.

Eastman, C. R. (transl. and ed.). 1900. Text-book of Paleontology (by K. A. Zittel). Macmillan & Co., London.

Feistmantel, O. 1873. Ueber den Nürschaner Gasschiefer, dessen geologische Stellung und organische Einschlüsse. Zeitschrift für deutsches geologisches Gesellschaft 25:593.

Fritsch, A. 1870. Ueber das Auffinden von neuen Thierresten aus der sogenannten Brettelkohle von Nyšan bei Pilsen. Stizungsberichte der Königlichen Böhmishen Gesellschaft der Wissenschaften. Prag 1870:33–49.

———. 1875. Přirodopsis živočišstva pro vyšši gymnasialni a realné školy. Prague.

———. 1876. Fauna der Steinkohlenformation Böhmens. Archiv für naturwissenschaftliche Landesdurchforschung von Böhmen. Prag 2: 1–15, 4 pls.

———. 1901. Fauna der Gaskohle und der Kalkstein der Permformation Böhmens 4:66–75. Prague.

Goldenburg, F. 1877. Fauna Sarepontana Fossilis. Die fossilen Thiere aus der Steinkohlenformation von Saarbrücken 2:35–36. Saarbrücken.

Grobben, K. 1919. Ueber die Musculatur des Vorderkopfes der Stomatopoden der Crustaceen. Sitzungsberichte der Akademie der Wissenschaften, Wien 101:237–274.

Haack, W. 1927. Zur Kenntnis des Syncariden *Uronectes (Gampsonyx) fimbriatus* Jorden aus

dem Rotliegenden. Preussisches geologisches Landesanstalt Jahrbuch 48:773–785.

Hessler, R. R. 1983. A defense of the caridoid facies; wherein the early evolution of the Eumalacostraca is discussed. Crustacean Issues 1: 145–164.

Johnson, R. G., and E. S. Richardson. 1966. A remarkable Pennsylvanian fauna from the Mazon Creek area, Illinois. Journal of Geology 74: 626–631.

Jordan, H. 1847. Entdeckung fossiler Crustaceen im Saarbrücken'schen Steinkohlengebirge. Verhandlungen des naturhistorischen Vereines preussischen Rheinlande 4:89–92.

Jordan, H., and H. von Meyer. 1854. Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. Palaeontographica 4:1–8.

Kent, L. S. 1982. Type and figured fossils in the Worthen collection at the Illinois State Geological Survey. Circular of the Illinois State Geological Survey 524:1–65.

Krejci, J. 1859. Eine neue Crustaces aus der böhmischen Steinkohlenformation. Lotos 9:79–80.

Kues, B. S., and K. H. Kitzke. 1981. A large assemblage of a new eurypterid from the Red Tanks Member, Madera Fm. of New Mexico. Journal of Paleontology 55:709–729.

Macmillan, D. L., G. Silvey, and I. S. Wilson. 1981. Coordination of the movements of appendages in the Tasmanian mountain shrimp *Anaspides tasmaniae*. Proceeding of the Royal Society of London (B)212:213–231.

Malzahn, E. 1958. Ein neuer jungpaläozoischer Krebs aus dem niederrheinischen Zechstein. Deutsche geologishe Gesellschaft Zeitschrift. 110:352–359.

Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. Paleontology 16: 713–719.

Meek, F. B., and A. H. Worthen. 1865. Notice of some new types of organic remains from the Coal Measures of Illinois. Proceedings of the Academy of Science, Philadelphia 1865:46–50.

Meek, F. G., and A. H. Worthen. 1866. Paleontology of Illinois. Descriptions of Invertebrates from the Carboniferous System. Geological Survey of Illinois 2:399–406.

——— and ———. 1868*a*. Preliminary notice of a scorpion, a *Eurypterus*?, and other fossils from the Coal Measures of Illinois. American Journal of Science (2)46:27–28.

——— and ———. 1868*b*. Paleontology of Illinois. Geological Survey of Illinois 3:289–565.

Mezzalira, S. 1946. Novos crustáceos Paleozoicos—crustáceos do Permiano de São Paulo, Brasil. Revista Instituto Geografico e Geologico, São Paulo 4:115–118.

———. 1948. Distribuição dos fôsseis do Estado de São Paulo. Mineraçãoe Metalurgia 13:249–255.

———. 1952. *Clarkecaris*, nova gênero de crustaceos Syncarida do Permiano. Boletim de Sociedade Brasileira de Geologia 1:46–51.

———. 1954. Novas ocorrências de crustáceos fósseis da Formação Irati do Sul do Brasil, pp. 165–170 *in* F. W. Lang (ed.). Paleontologia do Paraná. Comissão de Comemorações do Centennario do Paraná, Curitiba.

———. 1971. Contribução ao conhecimento da geologia de sub–superfície e da paleontologia da Formacao Irati, no Estado de São Paulo. Anais Academie Brasileira Ciências 43:273–336.

Noodt, W. 1963. Crustacea Syncarida de Chile central. Investigaciones Zoologicas Chilenas 10: 151–167.

———. 1965. Natürliches System und Biogeographie der Syncarida. Gewässer und Abwässer 37/38:77–186.

Packard, A. S. 1885. The Syncarida, a group of Carboniferous Crustacea. American Naturalist 19:700–703.

———. 1886*a*. On the Syncarida, a hitherto undescribed synthetic group of extinct malacostracous Crustacea. Memoirs of the National Academy of Science 3:123–128.

———. 1886*b*. On the Gampsonychidae, an undescribed family of fossil schizopod Crustacea. Memoirs of the National Academy of Science 3:129–133.

———. 1889. Paleontological Notes. Notes on Carboniferous arthropods from Illinois. Proceedings of the Boston Society of Natural History 24:211–213.

Paucaud, G., W. D. I. Rolfe, F. R. Schram, S. Secretan, and D. Sotty. 1981. Quelques invertébrés nouveaux du Stéphanien de Montceau-les-Mines. Bulletin de la Société d'Histoire Naturelle d'Autun 97:37–43.

Peach, B. N. 1908. Monograph on the higher Crustacea of the Carboniferous rocks of Scotland. Memoirs of the Geological Survey of Great Britain, Paleontology 1908:1–82. 12 pls.

———. 1914. On some Carboniferous arthropods with description of a new genus of myriapod. Proceedings of the Royal Physical Society 19: 142–148.

Pruvost, P. 1912. Note sur un myiapode du terrain houiller du Nord. Annales de la Société Geologique du Nord 41:65–69.

———. 1919. Introduction à l'étude du terrain houiller du Nord et du Pas-de-Calais. La faune continentale du terrain houiller du Nord de la France. Memoires pour Servir a l'Explication des Cartes Geologiques Detaillee de la France 1919:84–88.

———. 1922. Description d'un crustacé syncaride nouveau de l'assise de Chokier à Woensdrecht. Annales de la Société Scientifique de Bruxelles 42:147–150.

———. 1930. La faune continentale du terrain houiller de la Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 44:107–282, 14 pls.

Roemer, F. 1856. Palaeo-Lethaea: II. Theil. Kohlen-Periode (Silur-Devon-, Kohlen-, und Zechstein-Formation), pp. 672–675 *in* H. G. Bronn's Lethaea Geognostica. Bd.I. Stuttgart.

Rolfe, W. D. I. 1961. A syncarid crustacean from the Keele beds of Warwickshire. Paleontology 4:546–551.

———, F. R. Schram, G. Pacaud, D. Sotty, and S. Secretan. 1982. A remarkable Stephanian biota from Montceau-les-Mines, France. Journal of Paleontology 56:426–428.

Sayce, O. A. 1908. Description of a new remark-

able crustacean with primitive malacostracan characters. Annals and Magazine of Natural History 1(8):350–355.

Schminke, H. K. 1975. Phylogenie und Verbreitungsgeschichte der Syncarida. Verhandlungsbericht der deutschen zoologischen Gesellschaft 1974:384–388.

———. 1978. Die phylogenetische Stellung der Stygocarididae—unter besonderer Berücksichtigung morphologischer Ähnlichkeiten mit Larvenformen der Eucarida. Zeitschrift für zoologische Systematik und Evolutionsforschung 16:225–239.

———. 1981. Adaptation of Bathynellacea to life in the interstitial. Internationale Revue der gesamten Hydrobiologie 66:575–637.

Schneider, J., H. Walter, and J. Wunderlich. 1982. Zur Biostratinomie, Biofazies, und Stratigraphie des Unterrotliegenden der Breitenbacher Mulde (Thüringer Wald). Freiberger Forschungsheft 366:65–84.

Schram, F. R. 1969*a*. Stratigraphic distribution of Paleozoic Eumalacostraca. Fieldiana: Geology 12:213–234.

———. 1969*b*. Insights into the evolution of the Syncarida. Abstracts and Program of the Annual Meeting of the Geological Society of America 1969:12.

———. 1976*a*. Some notes on Pennsylvanian crustaceans of the Illinois basin. Fieldiana: Geology 35:21–28.

———. 1976*b*. Crustaceans from the Pennsylvanian Linton vertebrate beds of Ohio. Paleontology 19:411–412.

———. 1977. Palaeozoogeography of Late Paleozoic and Triassic Malacostraca. Systematic Zoology 26:367–379.

———. 1979*a*. British Carboniferous Malacostraca. Fieldiana: Geology 40:1–129.

———. 1979*b*. The Mazon Creek biota in the context of a Carboniferous faunal continuum, pp. 159–190 *in* M. H. Nitecki (ed.). *Mazon Creek Fossils*. Academic Press, New York.

———. 1981*a*. Late Paleozoic crustacean communities. Journal of Paleontology 55:126–137.

———. 1981*b*. Stalking wild mountain shrimp 'round the world. Part I. Environment Southwest 493:8–11.

———. 1981*c*. On the classification of the Eumalacostraca. Journal of Crustacean Biology 1: 1–10.

———. 1982. The fossil record and evolution of Crustacea, pp. 93–147 *in* L. G. Abele (ed.). The Biology of Crustacea Vol. I. Academic Press, New York.

———. 1983. Method and madness in phylogeny. Crustacean Issues 1:331–350.

———. 1984. Relationships within eumalacostracan Crustacea. Transactions of the San Diego Society of Natural History 20(16):301–312.

———, and J. M. Schram. 1979. Some shrimp of the Madero Formation (Pennsylvanian) Manzanita Mts., New Mexico. Journal of Paleontology 53:169–174.

Schram, J. M., and F. R. Schram. 1974. *Squillites spinosus* from the Mississippian Heath Shale of central Montana. Journal of Paleontology 48:95–104.

Scott, H. W. 1938. A stomatopod from the Mississippian of central Montana. Journal of Paleontology 12:508–510.

Scudder, S.H. 1882. Archipolypoda, a subordinal type of spined myriapods from the Carboniferous formation. Memoirs of the Boston Society of Natural History 3:143–182.

———. 1890. New Carboniferous Myriapoda from Illinois. Memoirs of the Boston Society of Natural History 4:417–442.

Secretan, S. 1967. Proposition d'une nouvelle compréhension et d'une nouvelle subdivision des Archaeostraca. Annales de Paléontologie 53:153–188.

———. 1972. A propos d'un nouvel exemplaire du Syncaride d'Autun: *Nectotelson rochei* Brocchi. Bulletin de la Société d'Histoire Naturelle d'Autun 64:9–12.

———. 1980*a*. Les arthropodes du Stephanien de Montceau-les-Mines. Bulletin Société d'Histoire Naturelle d'Autun 94:23–35.

———. 1980*b*. Comparison entre des crustacés a céphalon isolé, a propos d'un beau matériel de syncarides du Paléozoïque implications phylogéniques. Geobios 13:411–433.

Siewing, R. 1959. Syncarida. *in* H. G. Bronn, Klassen und Ordnungen des Tierreiches 5(1)4(2):1–121.

Smith, G. 1909. On the Anaspidacea, living and fossil. Quarterly Journal of Microscopical Science 53:489–578.

Thompson, G. M. 1893. Notes on Tasmanian Crustacea, with descriptions of new species. Proceedings of the Royal Society of Tasmania 1892:45–76.

———. 1894. On a freshwater schizopod from Tasmania. Transactions of the Linnean Society, Zoology 6:285–303.

Van Straelen, V. 1931. Crustacea Eumalacostraca (Crustaceis decapodis exclusis), pp. 1–98 *in* W. Quenstedt (ed.). Fossilium Catalogus I: Animalia. 48. W. Junk, Berlin.

Vandenberghe, A. 1960. Un arthropode du terrain houiller de la Loire *Eilecticus pruvosti*. Bulletin de la Société Geologique des France 11(7):690–692.

Vanhöffen, E. 1916. Die Anomostraken. Sitzungsberichte Gesellschaft naturforschender Freunde zu Berlin 1916:137–152.

Watling, L. 1981. An alternative phylogeny of peracarid crustaceans. Journal of Crustacean Biology 1:201–210.

———. 1983. Peracaridan disunity and its bearing on eumalacostracan phylogeny with a redefinition of eumalacostracan superorders. Crustacean Issues 1:213–228.

White, C. A. 1884. The fossils of the Indiana rocks. Reports of the Indiana Department of Geology and Natural History, Paleontology 13:107–180.

Wood, S. P. 1982. New basal Namurian (Upper Carboniferous) fishes and crustaceans found near Glasgow. Nature 297:574–577.

Woodward, H. 1881. Contributions to the study of fossil Crustacea. Geological Magazine (2)8: 529–534.

———. 1908. Some Coal Measure crustaceans with modern representatives. Geological Magazine (5)5:385–396.

———. 1911. On a large form of *Anthrapalaeman* from the clay–ironstone nodules of the Middle Coal Measures, Sparth Bottoms, Rochdale. Geological Magazine (5)8:361–366.

Zittel, K. A. 1885. Handbuch der Zoologie Band I, Abteilung 2, Lief 4. Oldenbourg, Munich and Leipzig.

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The Late Wisconsinan Vertebrate Fauna from Deadman Cave, Southern Arizona

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Abstract. We report a particularly rich assemblage of fossil vertebrates from a cave in southern Arizona. This fauna provides new data for reconstructing the inadequately known Late Pleistocene-Early Holocene biota of the Sonoran Desert and nearby mountains. The vertebrate fauna of Deadman Cave includes 5 amphibians, 25 reptiles (13 lizards and 12 snakes), 12 birds, and 22 mammals for a total of 64 species. Only one amphibian (*Bufo woodhousei*), three reptiles (*Callisaurus draconoides, Phrynosoma modestum, Gyalopium canum*), and one mammal (*Microtus* species) are locally extirpated, although all still occur in southern Arizona. An unidentified icterine bird may prove to be an extinct species. Extinct mammals include *Euceratherium collinum, Equus* species, and *Nothrotheriops shastensis*, all large herbivores. Other than the extinct animals, the fauna dating of the Late Pleistocene and Early Holocene is little different from that which is available in southern Arizona today. What appears to have changed is the mosaic of the plant and animal community. Distinctly boreal animals are lacking from the fauna. The climate during the time of deposition of the cave sediment appears to have been equable; certain animals now confined to deserts were able to live in more diverse woodland communities.

Introduction

Deadman Cave is a medium-sized, limestone cave at 1400 m (4600 ft) elevation on the northeastern side of the Santa Catalina Mountains, Pima County, Arizona (Fig. 1). The cave is located in the lower portion of the mountain range where various Paleozoic limestone formations are exposed and it appears to be formed in the Mississippian Escabrosa Formation (Wallace 1955).

The present vegetation of this highly dissected area is desert-grassland intermixed with the lower boundary of the oak woodland (*Quercus* species); juniper (*Juniperus erythrocarpa* and *J. deppeana*) is thinly scattered (Whittaker and Niering 1968). Desert-grassland elements such as agave (*Agave parryi*), ocotillo (*Fouqieria splendens*), variable prickly pear (*Opuntia phaeacantha*), and assorted grasses occur on the limestone and conglomerate hillslopes. Tributaries between the hills and the areas of the lower hillslopes are covered with velvet mesquite (*Prosopis velutina*), netleaf hackberry (*Celtis*

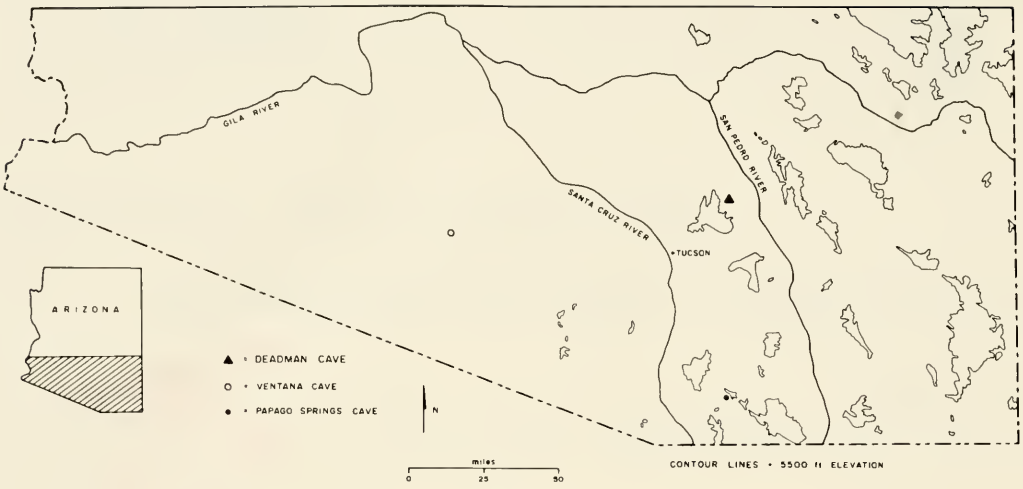

FIGURE 1. Map of southern Arizona with the locations of Deadman, Papago Springs, and Ventana caves. Contour lines (1650 m, 5500 ft) denote the positions of large mountain ranges, illustrating that southeastern Arizona is mountainous with great expanses of woodland and boreal habitats. The southwestern portion of the state contains predominately small desert mountains.

reticulata), and catclaw (*Acacia greggii*). The area around Deadman Cave is presently the ecotone between the creosotebush desertscrub communities of the San Pedro Valley (715 m elevation at the town of Mammoth) and the oak woodland above. Between Deadman Cave and the top of the Santa Catalina Mountains (2790 m elevation) there are Mexican pine-oak woodland, and ponderosa pine and mixed conifer forests.

The approximately three-by-five meter entrance to Deadman Cave is a collapsed cavern ceiling (Fig. 2). The cave once contained an elaborate system of active speleothems. Travertine building is now very rare to absent, possibly because of the development of the present entrance and resultant dessication; rimstone pools rarely contain any water (William Peachey 1980, *personal communication*).

During the late 1800s miners entered the cave to explore the numerous passages. A cabin was constructed across the entrance to the cave. Possibly at the same time, a shaft was begun in a back portion of the cave. This shaft penetrated a travertine surface layer and 2.4 m of cemented rubble containing bones, and provided access to a lower,

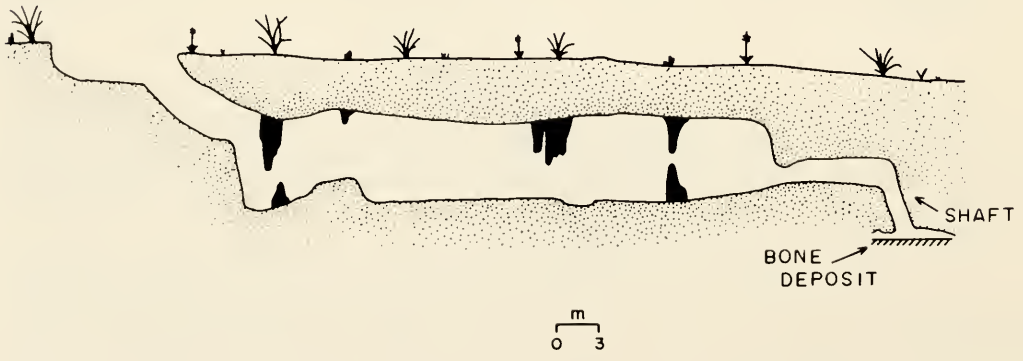

FIGURE 2. Generalized cross section of Deadman Cave, southern Arizona. The present entrance appears to have been the opening during the Late Pleistocene. A shaft built by miners during the 1800s cuts through two travertine layers and provides access to a lower room and the bone deposit, sealed off from the rest of the cave since approximately 8000 B.P.

sealed-off, small room. Here a second travertine layer covered a fine carbonate silt. At this point a trench was excavated horizontally through this loose sedimentary layer and then all mining operations ceased, leaving the exposed shaft and trench walls.

William Peachey informed us of the exposed sediments in Deadman Cave. One of us (ELR) and W. Peachey, entered the cave in 1972 and excavated an approximately 1.0 by 0.5 by 0.5 m layer of loose sediment from below the travertine layer capping the material exposed in the trench wall. All excavated sediments were screened through window mesh (2 mm) sieves. Most of the fossils were identified using the comparative collections at the University of Arizona, Tucson and the Division of Birds, Smithsonian Institution, Washington, D.C.

Chronology

The faunal assemblage contains three extinct species: the Shrub ox (*Euceratherium collinum*), the Shasta ground sloth (*Nothrotheriops shastensis*), and the Horse (*Equus* species). The remainder of the fauna can be found today living in various habitats in southern Arizona. *Euceratherium, Nothrotheriops,* and *Equus* apparently were extinct along with many other large mammals by approximately 11 000 to 10 200 B.P. (years before present; Martin 1967; Mosimann and Martin 1975; Haynes 1968; Meltzer and Mead 1983). The youngest known radiocarbon date on dung of *N. shastensis* is about 10 500 B.P. (Thompson et al. 1980). These dates suggest that at least some of the Deadman Cave faunal assemblage is of Late Wisconsinan age.

A radiocarbon date of 6080 ± 250 B.P. (A-1617) was determined on 14.8 grams of endocarps of *Celtis reticulata* found directly associated with the fauna. Unfortunately there was insufficient CO_2 available for a ^{13}C correction. *Celtis* endocarps are notorious for containing very little carbon and for being easily contaminated by carbonates in percolating water. The sediments had been leached of all organics; some of the bones were encrusted with carbonates. For this reason we believe that the ^{14}C age of 6000 B.P. is probably too young by at least 2000 years. The Deadman Cave faunal assemblage presented here most likely dates between 12 000 and 8000 B.P., grading across the Late Wisconsinan-Early Holocene boundary. Because of the uncertainties of the dating it is not possible to establish unequivocally whether all the reported taxa lived contemporaneously in the local community. The thick travertine cap and the sealing off of the lower room suggests that the deposit has not been contaminated with Middle or Late Holocene bones.

The Fossil Deposit

The fossiliferous layer is a pebbly silt (very pale brown, 7/3 10 YR dry, Munsell color) and shows no physical indication that the sediments were deposited by flowing water. The bones may have accumulated by a number of mechanisms. *Bassariscus astutus* (Ringtail) is a small carnivore that inhabits the cave today; small pockets of bones and seeds are presently developing as the scats of the Ringtail decay. Some of the fossil bone deposit in Deadman Cave may have been developed by the Ringtail as it was 2000 B.P. in Vulture Cave, Grand Canyon, Arizona (Mead and Van Devender 1981). *Spilogale putorius* (Spotted skunk) is the most common carnivore in the fossil deposit and it too may have helped in the accumulation of animal remains.

Owls (*Otus* species—Screech owl; *Micrathene whitneyi*—Elf owl; and *Asio otus*—Long-eared owl) were also recovered from the Deadman Cave deposit. The Long-eared owl is known to prey upon Spotted skunks and is the only owl that inhabits deep recesses in caves, that was recovered from the deposit.

The Ringtail and the Long-eared owl could very well account for the entire fossil deposit except for the larger mammal remains. The cave also may have been a den and a food cache for *Felis concolor* (Mountain lion) or other large carnivores, which could account for the occasional fossil remains of the Mountain lion, Horse, Ground sloth, and Shrub ox.

The area of the bone deposit (Fig. 2) is just beyond view of the light coming in

from the present and the presumed Late Wisconsinan-aged cave entrance. From here to the area of the fossil deposit, it is an easy passage for an owl or a mammalian carnivore, across an open, large cavern room. The predators may have had easy access to the lower room where the fossil bone deposit occurs, but the passage has since filled in with travertine, bones, and rock rubble.

Thus, the Deadman Cave fossil deposit is probably time transgressive by possibly a few thousand years, and appears to be an *in situ* deposit from the predator accumulation(s) dating some 8000 to 12 000 years ago.

Results

Fauna

The vertebrate fauna recovered from Deadman Cave (University of Arizona, Laboratory of Paleontology, UALP, locality 78121), is represented by 5 amphibians, 25 reptiles (13 lizards and 12 snakes), 12 birds, and 22 mammals, for a total of 64 species (Table 1).

The following is a systematic account of the fauna. After the skeletal element is the number of specimens, if more than one, and the UALP specimen number. "R" and "L" refer to right and left respectively. A brief discussion of identifying criteria and present-past distributions within the southwestern United States and northern Mexico is included. Our taxonomic sequences, distributional data, and descriptive osteological nomenclature is as follows: amphibians and reptiles—Stebbins (1966); birds—Baumel et al. (1979), Phillips et al. (1964); and mammals—Jones et al. (1982) for extant species and Kurtén and Anderson (1980) for extinct species. Amphibians and reptiles were identified by TRVD and JIM, birds by DWS, and mammals by ELR and JIM.

Class AMPHIBIA—Amphibians
Order ANURA —Toads and frogs
Family Pelobatidae—Spadefoot toads
Scaphiopus species—Spadefoot toad

Material.—Radio-ulna (11411).

Scaphiopus couchi—Couch's spadefoot toad

Material.—Vertebra (11409); R ilium (15312).

Remarks.— Skeletal elements from adult individuals of *Scaphiopus couchi* and *S. hammondi* are distinctive. The shape of the ilium, including the Ala ossa ilei and the Margo dorsalis, identify the fossil specimen as belonging to a spadefoot toad. *Scaphiopus couchi* may be distinguished from *S. hammondi* (Western spadefoot toad) by the following characters: 1) the area from the spina pelvis anterior to the acetabulum is relatively flat on *S. hammondi* but is raised at the acetabulum on *S. couchi*; 2) the articular surface at the acetabulum is curved on *S. hammondi,* but straight on *S. couchi*; and 3) the shape of the Spina pelvis posterior is angular on *S. hammondi,* but curved on *S. couchi. S. couchi* lives in a wide variety of desertscrub, grassland, and subtropical habitats including the Santa Catalina Mountains.

Amphibian subfossil and fossil remains are very inadequately represented in Arizona (Van Devender and Mead 1978, Mead 1981). Besides Deadman Cave, *S. couchi* is known from an Early Holocene age wood rat midden in Arizona (Van Devender and Mead 1978), Late Wisconsinan and Holocene cave deposits in southwestern New Mexico (Van Devender and Worthington 1977, Holman 1970, Brattstrom 1964), and from Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press).

Scaphiopus cf. *S. hammondi*—Western spadefoot toad

Material.—Vertebra (11410).

TABLE 1. Late Pleistocene, Holocene and present fauna from Deadman Cave and other localities in southern Arizona. Sequence and nomenclature is as follows (exceptions—see text): the amphibians and reptiles follow Stebbins (1966), the birds follow Phillips et al. (1964), and the mammals follow Jones et al. (1982) for the extant species and Kurtén and Anderson (1980) for the extinct species. 1 = Van Devender and Mead (1978); Van Devender (1973); Mead et al. (1983). 2 = Haury (1950). 3 = Skinner (1942) and Rea (1980). * = occurs in category. ! = extinct species. S.C.Mt. = Santa Catalina Mountains. ? = Questionable association.

	Present fauna			Wood rat middens[1]		Ventana Cave <10,000 B.P.[2]		Papago Springs Cave[3]
	S.C.Mt. or nearby valley	Southern Arizona	Deadman Cave	<10,000 B.P.	>10,000 B.P.	Volcanic unit	Conglomerate	Late Pleistocene
AMPHIBIANS								
Scaphiopus couchi	*	*	*	*				
S. cf. *S. hammondi*	*	*	*					
Bufo cf. *B. woodhousei*	*	*	*					
B. punctatus	*	*	*		*			
Rana sp.	*	*	*					
REPTILES								
Gopherus agassizi	?	*		*				
Coleonyx variegatus	?	*		*				
Sauromalus obesus		*		*	*			
Holbrookia maculata	*	*	*					
H. texana	*	*	*					
Callisaurus draconoides		*	*					
Crotaphytus collaris	*	*	*	*				
C. wislizeni		*			*			
Sceloporus cf. *S. magister*	*	*	*		*			
S. cf. *S. clarkii*	*	*	*					
S. cf. *S. undulatus*	*	*	*		*			
Uta stansburiana	*	*			*			
Urosaurus cf. *U. graciosus*	* ?	*		*				
U. ornatus	*	*	*					
Phrynosoma douglassi	*	*	*					
P. modestum		*	*					
P. solare	*	*	*					
Cnemidophorus cf. *C. tigris*	*	*		*	*			
Cnemidophorus sp.	*	*	*	*	*			
Heloderma suspectum	*	*	*					
Lichanura trivirgata	?	*			*			
Phyllorhynchus decurtatus	*	*		*	?			
Masticophis sp.	*	*	*	*	*			
Salvadora sp.	*	*	*					
Arizona elegans	*	*	*	*	*			
Pituophis melanoleucus	*	*	*	*	*			
Lampropeltis getulus	*	*	*		*			
L. pyromelana	*	*						
Rhinocheilus lecontei	*	*	*	*	*			
Sonora semianulata	*	*		*	*			
Chionactis occipitalis	*	*		*	*			
Gyalopium canum	*	*	*					
Trimorphodon biscutatus	*	*	*	*	*			
Hysiglena torquata	*	*	*	*	*			
Crotalus atrox	*	*	*		*			
C. cerastes	*	*			*			
C. scutulatus	*	*	*					

TABLE 1. Continued.

	Present fauna			Wood rat middens[1]		Ventana Cave		Papago Springs Cave[3]
						<10,000 B.P.[2]		
	S.C.Mt. or nearby valley	Southern Arizona	Deadman Cave	<10,000 B.P.	>10,000 B.P.	Volcanic unit	Conglomerate	Late Pleistocene
BIRDS								
Ibis-like								*
Colinus gambelii	*	*	*					
Colinus sp.	*	*	*					
Cyrtonyx montezumae	*	*	*					
Meleagris crassipes								*
Zenaida cf. *Z. macroura*	*	*	*					
Otus sp.	*	*	*					
Micrathene whitneyi	*	*	*					
Asio otus	*	*	*					
Caprimulgidae	*	*	*					
Colaptes auratus	*	*	*					
Turdus cf. *T. migratorius*	*	*	*					
Catharus guttatus	*	*	*					
Icterinae (probably extinct species)			*					
Emberizinae	*	*	*					
MAMMALS								
Notiosorex crawfordi	*	*	*	*	*			
Myotis cf. *M. velifer*	*	*						*
M. cf. *M. evotis*	*	*						*
M. cf. *M. thysanodes*								*
cf. *Myotis*	*	*	*					
Plecotus cf. *P. rafinesquii*	*	*						*
Antrozous pallidus	*	*	*	*				*
Tadarida cf. *T. brasiliensis*	*	*						*
!*Nothrotheriops shastensis*			*			*		
Sylvilagus auduboni	*	*						*
Sylvilagus sp.	*	*	*		*			
L. californicus	*	*				*		*
Lepus sp.	*	*	*	*	*			
Eutamias dorsalis	*	*						*
Eutamias sp.	*	*			*			
Marmota flaviventris								*
cf. *Ammospermophilus*	*	*		*				
Spermophilus variegatus	*	*	*					*
S. tereticaudus	*	*		*				
S. lateralis							*	
Cynomys ludovicianus		?				*		
Thomomys bottae or *umbrinus*	*	*						*
T. cf. *T. bottae*	*	*	*		*			
Perognathus cf. *P. flavescens*								*
P. cf. *P. flavus*	*	*	*					
P. baileyi	*	*		*				
Perognathus sp.	*	*		*	*			
Dipodomys spectabilis	*	*	*					
D. cf. *D. deserti*		*		*				
D. merriami	*	*		*	*			
Reithrodontomys montanus		*	*					

TABLE 1. Continued.

	Present fauna		Wood rat middens[1]			Ventana Cave <10,000 B.P.[2]		Papago Springs Cave[3] Late Pleistocene
	S.C.Mt. or nearby valley	Southern Arizona	Deadman Cave	<10,000 B.P.	>10,000 B.P.	Volcanic unit	Conglomerate	
Reithrodontomys sp.	*	*			*			
Peromyscus maniculatus	*	*						*
P. boylii or *truei*[3]	*/	*/*						*
Peromyscus sp.	*	*	*	*	*			
Onychomys torridus	*	*			*			
O. leucogaster		*						*
Sigmodon cf. *S. arizonae*	*	*	*	*	*			
S. ochrognathus		*			*			
Neotoma albigula	*	*	*		*			
N. lepida		*			*			
N. mexicana or *albigula*[3]	*/*	*/*						*
Microtus sp.		*	*					
M. cf. *M. mexicana*		*						*
Erethizon dorsatum	*	*			*			
Canis latrans	*	*					*	*
C. lupus		?						*
!*C. dirus*							*	
Vulpes macrotis	*	*					*	
Urocyon cinereoargenteus	*	*						*
Ursus americanus	*	*						*
Bassariscus astutus	*	*	*	*				
!*B. sonoitensis*								*
Taxidea taxus	*	*				*		*
Spilogale putorius	*	*	*					*
Mephitis mephitis	*	*						*
M. macroura	*	*	*					
Felis concolor	*	*	*					
!*Panthera leo atrox*						*		
!*Equus tau*								*
!*E. occidentalis*						*	*	
!*E. conversidens*								*
!*Equus* sp.			*					
!*Tapirus* sp.						*	*	
!*Platygonus compressus*								*
Dicotyles (=*Tayassu*) sp.	*	*				*		
!*Camelops* sp.								*
Odocoileus sp.	*	*	*			?		
Cervus sp.								*
!*Stockoceros* cf. *S. conklingi*						*	*	
!*S. onusrosagris*								*
!*Euceratherium collinum*			*					
Bison bison								*
Bison sp.							*	

Remarks.—The shape of centrum and the size of the fossil vertebra was indistinguishable with that of the Western spadefoot toad. *S. hammondi* is widely distributed in southeastern Arizona where it lives in desert, grassland, chaparral, woodland, and pine forest habitats (Lowe 1964). The fossil referred to as cf. *S. hammondi* represents

the first fossil occurrence for the species in Arizona. Late Pleistocene and/or Early Holocene age occurrences outside Arizona for this species are known from Nevada (Brattstrom 1976) and New Mexico (Holman 1970).

Family Bufonidae—Toads

Bufo cf. *B. woodhousei*—Woodhouse's toad

Material.—Vertebra (11408).

Remarks.—*Bufo woodehousei* is a large toad in relation to the other species found today in Arizona, although distinctly smaller than *B. alvarius* (Colorado River toad). *Bufo woodhousei* can be identified by: 1) the size is relatively larger at all stages of growth than most other *Bufo,* 2) the neural arch is higher making the centrum more pronounced, and 3) the articular facets are larger. Woodhouse's toad occurs in eastern and central Arizona and in isolated populations in the Yuma area of southwestern Arizona. In southern Arizona *B. w. australis* is primarily a riparian species restricted to permanent or semi-permanent streams. Late Pleistocene or Early Holocene age remains of *Bufo woodhousei* have not been previously reported from Arizona. Outside Arizona, fossil remains of this toad are known from Nevada (Mead et al. 1982) and New Mexico (Holman 1970).

Bufo punctatus—Red-spotted toad

Material.—Urostyle (15002).

Remarks.—*Bufo punctatus* is a small toad with many easily identifiable skeletal elements. The paired anterior condyles of the urostyle are relatively broad, flat ovals as in *B. punctatus.* Juveniles of the larger species of *Bufo,* do not have as flattened an anterior end to the urostyle. This xeric-adapted toad occurs throughout most of the Southwest, living in habitats ranging from desertscrub to Mexican pine-oak woodland. Late Pleistocene remains of *B. punctatus* occur in three Arizona localities (Van Devender and Mead 1978), New Mexico (Holman 1970, Van Devender and Worthington 1977), and Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press).

Family Ranidae—Frogs

Rana species—Frog

Material.—Humerus (11412).

Remarks.—The long, slender humerus is identifiable to *Rana,* but we were only able to identify the fossil to a small species. *Rana pipiens* (Leopard frog) and *R. tarahumarae* (Tarahumara frog) along with the introduced *R. catesbeiana* (Bull frog) occur in southern Arizona today. Only *R. pipiens* and the introduced species occur near Deadman Cave where they are restricted to permanent water habitats along streams. *Rana* species have been recovered as Quaternary fossils in California (Brattstrom 1953*a, b,* Hudson and Brattstrom 1977), Nevada (Brattstrom 1954), New Mexico (Holman 1970, Van Devender and Worthington 1977), and Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press).

Class REPTILIA—Reptiles

Order SQUAMATA—Lizards and Snakes

Suborder Sauria—Lizards

Family Iguanidae—Iguanid lizards

Holbrookia maculata—Lesser earless lizard

Material.—Dentary (11394).

Remarks.—The Lesser earless lizard is a small ground-dwelling lizard common in open habitats of desertscrub, desert grassland, and oak woodlands. It lives in the lower elevations of the Santa Catalina Mountains and occurs over most of eastern Arizona (Lowe 1964). The only previous Late Pleistocene and Early Holocene records of this lizard are from New Mexico (Van Devender and Worthington 1977).

Holbrookia texana—Greater earless lizard

Material.—R & L dentaries (2; 11401); R maxilla (11395).

Remarks.—Teeth of *H. texana* are relatively taller on a deeper dentary than those of the smaller *H. maculata.* Dentaries of *Holbrookia* have a closed but not fused Meckel's canal. Today this lizard is found in open habitats on the south side of the Santa Catalina Mountains, but not near the cave at present. This insectivorous lizard lives at middle elevations in west central and southern Arizona, avoiding extreme desert lowlands (Stebbins 1966, Lowe 1964). The only other known Late Pleistocene or Early Holocene records of this lizard are from New Mexico (Van Devender and Worthington 1977).

Callisaurus draconoides—Zebra-tailed lizard

Material.—L dentaries (2; 11386).

Remarks.—Teeth and dentaries of *Callisaurus draconoides* are similar to those of most medium-sized sceloporine lizards and to *Holbrookia* in particular, but they can be differentiated using an ontogenetic size series of specimens. Dentaries and teeth of *Callisaurus* are much larger and more robust than those of species of *Holbrookia*; osteologically *Callisaurus* is most similar to *H. texana.* The anterior one third of the *Callisaurus* dentary is very slender and has a more medial, internal, orientation to Meckel's canal, as compared to the more ventral orientation of either *Holbrookia* or *Sceloporus.* The Zebra-tailed lizard lives in regions of fairly open sandy or gravelly, low-elevation, desertscrub communities. The nearest population to Deadman Cave is in the low areas near Florence Junction and along the San Pedro River. This is the first Late Pleistocene-Early Holocene record of *C. draconoides.*

Crotaphytus collaris—Collared lizard

Material.—R & L dentaries (6; 11390); R & L maxillae (8; 11391); pterygoid (11392); frontal (15003).

Remarks.—Specimens of *C. collaris* and *C. wislizeni* (Leopard lizard) can be separated from most other iguanid lizards by their overall larger size, and the tendency for the teeth to be pointed and recurved, an adaptation for their carnivorous habits. The teeth of *C. collaris* are relatively wider anteroposteriorly than those of *C. wislizeni,* with the posterior teeth strongly tricuspid and the anterior teeth being more like blunt cones with a slight posterior curve. Both the pterygoid and the frontal are more rugose on *C. collaris* than they are on *C. wislizeni.*

We use the name *Crotaphytus collaris* (*sensu lato*) and have not tried to separate *C. collaris* from *C. insularis* (Smith and Tanner 1972, Montanucci et al. 1975). Collared lizards can be found in all mountainous regions of southern Arizona and occasionally on open flat terrain (Lowe 1964). It presently lives near Deadman Cave.

The Collared lizard is known from fossil sites in Arizona (Van Devender and Mead 1978, Mead 1981, Cole and Mead 1981), Nevada (Brattstrom 1954*a*, Mead et al. 1982), New Mexico (Holman 1970, Gehlbach and Holman 1974, Van Devender and Worthington 1977).

Sceloporus cf. *S. clarkii*—Clark's spiny lizard

Material.—L dentaries (2; 11396); R & L maxillae (2; 11397).

Sceloporus cf. *S. magister*—Desert spiny lizard

Material.—R & L dentaries (2; 11398).

Sceloporus clarkii or *magister*—Clark's or Desert spiny lizard

Material.—R & L dentaries (10; 11400); R & L maxillae (9; 11399).

Remarks.—Osteologically it is difficult to distinguish these two moderately large

spiny lizards in their southeastern Arizona range. *Sceloporus magister* can have more robust dental characters. It usually inhabits the low deserts but will occur up into the desert–grassland. *Sceloporus clarkii* lives in woodlands in Arizona, but is a common inhabitant in the subtropical thornscrub in Sonora, Mexico. Both species are found today in the Santa Catalina Mountains. Other Late Pleistocene and/or Early Holocene records of Clark's spiny lizard are in New Mexico (Van Devender and Worthington 1977) and Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press). *Sceloporus magister* is fairly common in the fossil record, including Arizona (Van Devender and Mead 1978, Mead 1981), California (Brattstrom 1953*a, b*), and New Mexico (Van Devender and Worthington 1977).

Sceloporus cf. *S. undulatus*—Eastern fence lizard

Material.—R & L maxillae (3; 11387); R dentaries (2).

Remarks.—These specimens are from a small species of *Sceloporus* similar to either *S. undulatus* or *S. occidentalis* (Western fence lizard). They can be distinguished from juvenile *S. magister* or *S. clarkii* by their more slender, taller teeth. Maxillae and dentaries are less rugose in the Fence lizard, but are larger in all aspects than the *S. graciosus* (Sagebrush lizard). We are not convinced that *S. undulatus, S. occidentalis,* or *S. virgatus* (Striped Plateau lizard) can be reliably separated satisfactorily on skeletal fragments.

Sceloporus undulatus presently occurs near the cave, while *S. occidentalis* and *S. graciosus* occur farther north and *S. virgatus* occurs in southeasternmost Arizona. For this reason the material may be referred to *S. undulatus.* The Eastern fence lizard habitat in Arizona ranges from forested mountains down into the desert-grassland.

Remains of *S. undulatus* are known from Late Pleistocene and Early Holocene deposits in Arizona (Van Devender and Mead 1978, Mead 1981, Cole and Mead 1981) and New Mexico (Holman 1970, Van Devender and Worthington 1977).

Urosaurus ornatus—Tree lizard

Material.—L dentary (11402).

Remarks.—*Urosaurus ornatus* may be differentiated from most small iguanids including *U. graciosus* (Long-tailed Brush lizard) by its more slender teeth and the presence of a small fused area of the Meckel's canal. The Tree lizard in Arizona occurs in a wide variety of habitats from low, hot deserts up to open pine-oak woodlands. Late Pleistocene–Early Holocene remains of the Tree lizard have been found in southwestern New Mexico (Van Devender and Worthington 1977). The Deadman Cave specimen is the first fossil record for the species in Arizona.

Phrynosoma douglassi—Short-horned lizard

Material.—R & L dentaries (6; 11385); R & L maxillae (8; 11384).

Phrynosoma modestum—Round-tailed horned lizard

Material.—R dentary (11382); L maxilla (11383); parietal (3; 15004–15006).

Phrynosoma solare—Regal horned lizard

Material.—Parietal (11381); angular (15007); squamosal (15008).

Remarks.—Species of *Phrynosoma* can be differentiated from one another by most bones of the skull, especially those which bear horns (*see* Figs. 1–8 in Reeve 1952). The dentary, maxilla, and parietal are very rugose in *P. modestum* and are easily differentiated from the similar species, *P. platyrhinos* (Desert horned lizard), which lacks rugosity. Size, shape, and ornateness will differentiate *P. solare* from other species (*see* also Reeve 1952).

Phrynosoma douglassi presently occurs in the higher forests, woodlands, and grass-

land habitats in eastern Arizona and the Santa Catalina Mountains, whereas, *P. solare* lives in the Sonoran Desert valleys and bajadas, and adjacent desert-grasslands. *Phrynosoma modestum* is a characteristic Chihuahuan Desert animal found in desertscrub and desert-grassland habitats. Today it occurs no further west than Sulphur Springs Valley, 95 km east of the San Pedro River Valley. This is the first fossil record for *P. solare*; *Phrynosoma modestum* is recorded from New Mexico (Van Devender and Worthington 1977); *P. douglassi* is recorded from New Mexico (Gehlbach and Holman 1974, Van Devender and Worthington 1977) and Nevada (Mead et al. 1982).

Family Teiidae—Teiid lizards
Cnemidophorus species—Whiptail lizard

Material.—L dentary (11389); L maxilla (11388).

Remarks.—Neither the dentary nor the maxilla allowed for specific identification. Five species of Whiptail lizards occur in southern Arizona (*C. burti, C. exanguis, C. arizonae, C. inornatus,* and *C. tigris*).

Family Helodermatidae—Beaded lizards
Heloderma suspectum—Gila monster

Material.—Vertebra (11393).

Remarks.—Vertebrae of *Heloderma* can be separated from the only other large lizard of comparable size in Arizona, *Sauromalus obesus* (Chuckwalla), because they lack zygantra and zygosphenes and the dorsal half of the cotyle is oval rather than subsquare to orbicular.

The Gila monster occurs in Arizona from the southern half of the state north into the extreme northwestern corner. Living primarily in the lowlands of the Sonoran Desert and portions of the Mohave Desert, the venomous Gila monster also occurs less commonly in desert-grasslands, and rarely in the oak woodlands. *Heloderma suspectum* is common along the lower portions of the Santa Catalina Mountains but probably does not occur today at Deadman Cave.

It is not known whether the Gila monster occurred in Arizona, California, and Nevada during the Late Wisconsinan glacial or if it was a Holocene immigrant from the Sonoran Desert lowlands in the Lower Colorado River Valley around the head of the Gulf of California in Sonora, Mexico. Inadequately dated Late Pleistocene-Holocene remains occur at Vulture Cave, Arizona, and Gypsum Cave, Nevada (Mead and Phillips 1981, Brattstrom 1954*a*).

Suborder Serpentes—Snakes
Family Colubridae—Colubrid snakes
Masticophis species—Racer

Material.—Vertebrae (11; 11404).

Remarks.—The vertebrae of *Masticophis* are similar to those of *Coluber* (Racer) and *Salvadora* (Patch-nosed snake) (*see* the remarks under the latter species). *Masticophis* may be identified by the following: 1) the cotyle-condyle length (cl) is up to 6.5 mm, occasionally to 8.2 mm, 2) the ratio of the cotyle-condyle length in relation to the neural arch width (NAW) is between 1.48 and 1.75, 3) the accessory process is long, pointed, and mostly oblique to anterior, and 4) the ratio of the distance between the prezygapophyses (PR-PR) and that distance between the prezygapophysis and the postzygapophysis (PR-PO) is between 0.87 and 1.00. This same ratio for *Coluber* is 0.98 to 1.25 (Auffenberg 1963).

Snakes of the genus *Masticophis* are large, active, diurnal predators. Within the genus, identification to species is difficult; the vertebrae of *Coluber constrictor* (Blue Racer) are similar as well. *Masticophis flagellum* (Coachwhip) and *M. bilineatus* (Sonoran whipsnake) occur near Deadman Cave, while *M. taeniatus* (Striped whipsnake) occurs in the mountains to the north and northeast. Late Wisconsinan and Early

Holocene remains of *Masticophis* species are known from New Mexico (Van Devender and Worthington 1977), Arizona, and California (Van Devender and Mead 1978), Nevada (Mead et al. 1982) and from the interglacial age Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press).

Salvadora species—Patch-nosed snake

Material.—Vertebrae (3; 11405).

Remarks.—The vertebrae of *Salvadora* are similar to those of *Coluber* and *Masticophis.* All generally have thin dorsal spines, a well-defined, thin haemal keel, and a tendency for epizygapophyseal spines. *Salvadora* is different from the latter two species in having a relatively smaller neural canal and a smaller condyle (Holman 1962). We do not know of any vertebral characters that unequivocally separate the two species within this genus. Snakes of the genus *Salvadora* are small ground dwellers. *S. grahamiae* (Mountain patch-nosed snake) occurs in the mountains of southeastern Arizona in oak woodlands and above, whereas *S. hexalepis* (Desert patch-nosed snake) is widely distributed in southern and western Arizona, living below the chaparral and woodland edge. Both species live in the Santa Catalina Mountains. The genus was recovered from the inter-glacial deposit at Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press) and from a Late Wisconsinan-Early Holocene cave deposit in New Mexico (Van Devender and Worthington 1977).

Arizona elegans—Glossy snake

Material.—Vertebrae (9; 11413).

Remarks.—Characters used to identify the vertebrae of *A. elegans* are: 1) the cl is up to 3.5 mm, 2) the ratio of cl and NAW is between 1.08 and 1.25, 3) the high neural arch, 4) the neural spine is high and moderately thin, 5) there is a long thin accessory process which is rounded and oblique to the anterior, and 6) the cotyle is oval to subround (Van Devender and Mead 1978). This medium-sized nocturnal snake lives in deserts and grasslands of most of the Southwest as well as in northern Mexico. This snake is known from Late Wisconsinan and Early Holocene remains in New Mexico (Van Devender and Worthington 1977) and Arizona (Van Devender and Mead 1978).

Pituophis melanoleucus—Bull or Gopher snake

Material.—Vertebrae (10; 11418).

Remarks.—Criteria for identification are discussed in Auffenberg (1963), but those used here are: 1) the cl is up to 7.5 mm, 2) the cl/NAW ratio between 1.07 and 1.17, 3) the neural arch is very high with the neural spine being high and thick, 4) the zygosphene is moderately or strongly convex from the anterior, 5) the accessory processes are short, pointed or blade-like, and 6) the cotyle is round, relatively large, and only slightly oblique (Van Devender and Mead 1978). *Pituophis melanoleucus* is a widespread North American snake that lives in a wide variety of habitats in Arizona up to about 3000 m (9900 ft). Fossils of the species are found in Arizona (Van Devender et al. 1977, Van Devender and Mead 1978, Mead 1981, Cole and Mead 1981), California (Brattstrom 1953*a*), Nevada (Brattstrom 1958, 1976, Mead et al. 1982), and New Mexico (Van Devender and Worthington 1977).

Lampropeltis getulus—Common king snake

Material.—Vertebrae (7; 11416).

Remarks.—For the species identification characters, see *L. pyromelana.* Fossils of *L. getulus* are known from Arizona (Van Devender et al. 1977, Van Devender and Mead 1978, Mead and Phillips 1981, Mead 1981), California (Brattstrom 1976, Van Devender and Worthington 1977).

Lampropeltis pyromelana—Sonoran mountain kingsnake

Material.—Vertebrae (8; 11417).

Remarks.—The haemal keel and subcentral ridges are well developed in the kingsnakes. *Lampropeltis getulus* is a large species and has a sharp neural spine with relatively blunt accessory processes. *Lampropeltis pyromelana* is a small species and has a thin, low neural spine and has short, pointed accessory processes. Both species occur in the Santa Catalina Mountains. *L. getulus* is common over most of North America, whereas *L. pyromelana* is found in montane habits in Nevada, Utah, and south into Mexico. Fossil remains have been reported from New Mexico (Van Devender and Worthington 1977) and Nevada (Mead et al. 1982).

Rhinocheilus lecontei—Long-nosed snake

Material.—Vertebrae (22; 11419).

Remarks.—Although vertebrae of *R. lecontei* superficially resemble those of *Lampropeltis getulus,* they are readily distinguished using the following criteria: 1) the cl is up to 3.0 mm, 2) the ratio of the cl and the NAW is between 1.07 and 1.21, 3) the neural spine is often flat-topped, 4) the zygosphene is often flat from the anterior, 5) the accessory process is blunt, lateral or dorsal from the anterior, 6) the cotyle is round and narrower than the zygosphene, and 7) the subcentral ridges are well-developed, but less so than in *Lampropletis getulus* (Auffenberg 1963, Hill 1971, and Van Devender and Mead 1978). This medium-sized, nocturnal snake is widespread in desert, grassland, subtropical thornscrub habitats in the Southwestern U.S. and northern Mexico. The snake probably occurs near the cave today. Late Pleistocene–Holocene fossils occur in New Mexico (Van Devender and Worthington 1977), Arizona and California (Van Devender and Mead 1978, Mead 1981) and Nevada (Mead et al. 1982).

Gyalopium canum—Western hook-nosed snake

Material.—Vertebra (11414).

Remarks.—Vertebrae of *Gyalopium canum* are small but very broad for their length. The haemel keel is poorly developed and the cotyle and condyle are relatively large compared to those of *Sonora semiannulata* (Ground snake) and *Chionactis occipitalis* (Banded sand snake).

The Western hook-nosed snake is a small snake that lives in the desertscrub and desert-grasslands from southeastern Arizona to Trans-Pecos, Texas and south into the Chihuahuan Desert of Mexico. Presently it occurs no closer to Deadman Cave than the Santa Rita Mountains, 80 km to the south. The only previous fossil record of the species (as *Ficimia cana*) was from New Mexico (Van Devender and Worthington 1977).

Trimorphodon biscutatus—Lyre snake

Material.—Vertebrae (105; 11420).

Remarks.—Criteria for the identification of *T. biscutatus* are as follows: 1) the cl is up to 4.5 mm, 2) the cl/NAW ratio is between 1.08 and 1.25, 3) the neural arch is flattened, 4) the neural canal is relatively small, 5) the zygosphene is relatively small, 6) the accessory process is short and pointed, 7) the cotyle is oval to subround, strongly oblique, narrower than the zygosphene, and 8) the haemal keel is well-developed but low (Van Devender and Mead 1978). The Lyre snake is a medium-sized species that lives in desertscrub habitats in the Southwest and northern Mexico. It is found near Deadman Cave today. Fossils occur in New Mexico (Van Devender and Worthington 1977), Arizona, and California (Van Devender and Mead 1978).

Hypsiglena torquata—Night snake

Material.—Vertebrae (12; 11403, 11415).

Remarks.—Criteria for identification are as follows: 1) the cl is between 1.65 and 2.75 mm, 2) the cl/NAW ratio is 1.18 to 1.31, 3) the neural arch is moderately depressed from the posterior, 4) the neural spine is low, usually with the dorsal edge thickened and the anterior corner is bifurcate, 5) the accessory process is lateral from the anterior, and 6) the cotyle is relatively small (Van Devender and Mead 1978). The Night snake is widespread in desert, grassland, and woodland habitats in the Southwestern U.S. and northern Mexico. It occurs today near Deadman Cave. Fossils are known from New Mexico (Van Devender and Worthington 1977), Arizona and California (Van Devender and Mead 1978, Mead 1981), Nevada (Mead et al. 1982), and Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press).

Family Viperidae (= Crotalidae)—Pit vipers

Crotalus atrox—Western diamondback rattlesnake

Material.—Vertebrae (5; 11406).

Remarks.—The thoracic vertebrae of the Viperidae are distinct from those of the Colubridae and Boidae in that they have a long, pointed hypophysis. The fossil vertebrae are from a large rattlesnake resembling *C. atrox*; other rattlesnakes in Arizona generally do not attain its size, except for some *C. molossus* (Blacktailed rattlesnake). Both species occur near Deadman Cave. *Crotalus atrox* is a large desert species usually occuring in the lower valleys, whereas, *C. molossus* is a woodland-dwelling species that is occasionally found in rocky habitats in more xeric desert mountain ranges. Late Pleistocene fossils of *C. atrox* have been reported from Gypsum Cave, Nevada (Brattstrom 1954*a, b*) and Conkling Cavern, Shelter, Fosbert (Brattstrom 1964) and Dry caves, New Mexico (Holman 1970). There are no unequivocal records of fossil *C. atrox* from Arizona; however, there is the interglacial record from Rancho la Brisca, Sonora, Mexico (Van Devender et al. in press).

Crotalus scutulatus—Mohave rattlesnake

Material.—Vertebrae (3; 11407).

Remarks.—The fossil vertebrae are from a medium-sized rattlesnake that is smaller than *Crotalus atrox* or *C. molossus*. The vertebrae of *C. viridus cerberus* (Arizona black rattlesnake), a common snake in the oak woodland, differ from those of *C. scutulatus* in their relative size of the hypophysis (*see* also Brattstrom 1964*b*). The vertebrae of *C. cerastes* (Sidewinder), *C. lepidus* (Rock rattlesnake), *C. pricei* (Twin spotted rattlesnake), and *C. willardi* (Ridgenosed rattlesnake) are smaller and differ in various morphological characters. The Mohave rattlesnake is a common desert-grassland and desertscrub snake in southern Arizona and near Deadman Cave today. Fossils of *C. scutulatus* have not been reported previously.

Class AVES—Birds

Order GALLIFORMES—Gallinaceous birds

Family Phasianidae— Pheasants, quails, etc.

Colinus gambelii—Gambel's quail

Material.—Complete carpometacarpus (15313).

Remarks.—This specimen is much smaller than the carpometacarpi of *C.* ("*Oreortyx*") *pictus* (Mountain quail) or *Cyrtonyx montezumae* (Harlequin quail), and is slightly smaller than that in *C.* ("*Callipepla*") *squamata* (Scaled quail). It differs from *C. squamata* and *C. virginianus* (Bobwhite) in having the Os metacarpale minus (metacarpal III) more slender and more curved in caudal aspect, and in having a slightly smaller Processes extensorius. This is only the second fossil occurrence of *C. gambelii,* the other being from the Early Pleistocene (Irvingtonian) of Vallecito Creek, California (Howard 1963). Brodkorb (1964) listed *C. gambelii* questionably from Conkling Cavern and Shelter Cave, New Mexico. These assignments conflict, however, with the original references, as Howard and A. H. Miller (1933) reported "*Lophortyx* sp. Quail"

(sic) from these two sites. Gambel's quail lives today in the vicinity of Deadman Cave, but is approximately at its upper elevational limit.

Colinus species—quail

Material.—Proximal and distal ends of humeri (15009).

Remarks.—Among quail of the Southwest, these specimens are smaller than the humeri of *Colinus* ("*Oreortyx*") *pictus* or *Cyrtonyx montezumae.* We cannot, however, distinguish them from humeri of *Colinus virginianus, C.* ("*Lophortyx*") *gambelii,* or *C.* ("*Callipepla*") *squamata,* any of which could have occurred at Deadman Cave. Although species-level identifications are often very difficult, quail of the genus *Colinus* are common as Pleistocene fossils in southern North America, especially Florida, New Mexico, and California.

Cyrtonyx montezumae—Harlequin quail

Material.—Proximal end with partial shaft of radius (15010).

Remarks.—This specimen is larger than the radius in all other southwestern quail except *Colinus pictus.* It is referable to *Cyrtonyx* by the less expanded articulating surface of the proximal end relative to the width of the shaft. The only other fossil occurrence of *C. montezumae* is at San Josecito Cave, Nuevo Leon, Mexico (L. Miller 1943), also of Late Pleistocene age. Today the Harlequin quail occurs in grassy mountain woodlands of central and southeastern Arizona, thence ranging south well into Mexico. This species is very characteristic of evergreen oak grassland and is at its lower elevational limit near Deadman Cave today. With the historical reduction of grass and increase in brush at mid-elevations in Arizona mountains, this once common bird has decreased in abundance.

Order COLUMBIFORMES—Pigeons and doves
Family Columbidae—Pigeons and doves
Zenaida cf. *Z. macroura*—Mourning dove

Material.—Proximal end of carpometacarpus (15011).

Remarks.—This fossil differs markedly in size from the carpometacarpi of all Arizona columbids except *Zenaida macroura* and *Z. asiatica* (White-winged dove). It is tentatively assigned to *Z. macroura* in being slightly smaller than all available specimens of *Z. asiatica.* This is the first Pleistocene record of *Z. macroura* in Arizona, although this species is a fairly common Late Pleistocene fossil elsewhere in North America. The Mourning dove is very widespread in Arizona, both geographically and altitudinally, and thus is of little paleoecological interest.

Order STRIGIFORMES—Owls
Family Strigidae—Typical owls
Otus species—Screech-owl

Material.—Two proximal ends and one distal end of humeri (3; 15012), proximal end of carpometacarpus (15013).

Remarks.—These specimens all agree in size and morphology with *Otus asio* (Common screech-owl), and are either larger or smaller than in all Arizonan owls outside of the genus *Otus.* The carpometacarpus and one proximal end of humerus are slightly larger than in *O. flammeolus* (Flammulated screech-owl), but the other elements resemble both *O. asio* and *O. flammeolus.* No skeleton was available for *O. trichopsis* (Spotted screech-owl), so identification beyond generic level is not possible. These three species of *Otus* in Arizona are largely separated from each other today by habitat and elevation, and it seems most likely that *O. asio* or *O. trichopsis* would have lived near Deadman Cave in the Late Pleistocene. Probably only *O. asio* occurs in the immediate vicinity of Deadman Cave today. *Otus asio* is a common Late Pleistocene fossil in

North America, while *O. flammeolus* and *O. trichopsis* have only two and one Pleistocene records, respectively. This is the first fossil record of *Otus* in Arizona.

Micrathene whitneyi—Elf owl

Material.—Proximal end of humerus (15014), distal end of tarsometatarsus (15015).

Remarks.—The Elf owl is readily separated from all other owls by its extremely small size. This is the first Pleistocene record for *M. whitneyi.* It occurs today in the region of Deadman Cave, nesting in holes in trees at any elevation "below the heavy pine forest" (Phillips et al. 1964).

Asio otus—Long-eared owl

Material.—Distal end of humerus (15016).

Remarks.—This fossil agrees with the humerus of *Asio otus* versus *A. flammeus* (Short-eared owl) in having a distinctive knot-like ectepicondylar prominence (Processes supracondylaris dorsalis). *Asio otus* is a fairly common Late Pleistocene fossil in western North America, but this is the first such record in Arizona. The Long-eared owl is not unexpected at Deadman Cave, as it occurs today in Arizona in a variety of habitats, both as a nesting bird and a winter visitor. As mentioned above, *A. otus* probably was involved in the accumulation of small vertebrates in Deadman Cave.

Order CAPRIMULGIFORMES—Goatsuckers, etc.
Family Caprimulgidae—Night jars
Genus and species indeterminate

Material.—Carpometacarpus lacking distal end and much of metacarpal III (15017).

Remarks.—This carpometacarpus is distinguished from that of *Chordeiles minor* (Common nighthawk) and *C. acutipennis* (Lesser nighthawk) by its much smaller size, and from *Caprimulgus vociferus* (Whip-poor-will) by its slightly smaller overall size with a more slender metacarpal III. It resembles that of *Phalaenoptilus nuttallii* (Poor-will) very closely, but the shape of metacarpal I is somewhat more similar to that in *Caprimulgus.* In the absence of a comparative skeleton of *Caprimulgus ridgwayi* (Ridgeway's whip-poor-will), the only other caprimulgid living in Arizona, precise identification of this fossil is impossible. The Pleistocene record of caprimulgids is poorly known everywhere. This is the first fossil record for the family in Arizona.

Order PICIFORMES—Woodpeckers, etc.
Family Picidae—Woodpeckers
Colaptes auratus—Flicker

Material.—Distal end of tarsometatarsus (15018).

Remarks.—Among Arizonan woodpeckers, the tarsometatarsus of *Colaptes auratus* is similar in size only to that of *Melanerpes* ("*Asyndesmus*") *lewis* (Lewis' woodpecker). The fossil agrees with *C. auratus* versus *M. lewis* in its larger, less deeply sculptured middle trochlea. The distal end of the tarsometatarsus in the "Red-shafted" flicker (*C. a. collaris*) appears to be indistinguishable from that in the "Gilded" flicker (*C. a. mearnsi*). Thus the fossil provides no evidence of paleohabitats near Deadman Cave. *C. a. collaris* is a bird of mountain woodland and forest, ranging upward from approximately 1220 m elevation, whereas *C. a. mearnsi* occurs in desertscrub, generally below 1370 m elevation. Based on the remainder of the avifauna, one would guess that the Late Pleistocene flicker at Deadman Cave was *C. a. collaris,* although both forms occur in the general region of the site today. Flickers are very common Late Pleistocene fossils, yet once again this is the first such record for Arizona.

Order PASSERIFORMES—Perching birds
Family Turdidae—Thrushes
Turdus cf. *T. migratorius*—American robin

Material.—Proximal end of humerus (15019).

Remarks.—The humerus of *Turdus migratorius* can be told from that of most other North American turdids by its larger size. It can be recognized from that in *Ixoreus naevius* (Varied thrush) by its stouter Crus dorsalis fossae which, along with the deeper dorsal Fossa pneumotricipitalis, also distinguishes it from the humeri of mimids (thrashers, mockingbirds). The humerus of *T. migratorius* can be separated from that in the neotropical *T. grayi* (Clay-colored robin) reported from Stanton's Cave, Coconino County, Arizona (Rea and Hargrave, ms) by its lesser degree of pneumaticity in both the dorsal and ventral Fossa pneumotricipitalis, the former also being larger in *T. grayi*. The fossil differs from the only available humerus of *T. rufopalliatus* (Rufous backed robin, a vagrant to Arizona today; resident in Sonora) in having a larger and more oblong (less circular) opening of the ventral Fossa pneumotricipitalis. Lacking additional specimens of *T. rufopalliatus* to confirm this character, no more than a tentative assignment of the fossil to *T. migratorius* is warranted. *T. migratorius* is a common Late Pleistocene species in much of North America, and has been reported in Arizona from Stanton's Cave (Rea and Hargrave, ms). The American robin is common in Arizona today, nesting throughout the state in wooded regions above approximately 1220 m elevation.

Catharus guttatus—Hermit thrush

Material.—Distal end of humerus with most of shaft (19020).

Remarks.—The humerus of *Catharus guttatus* is smaller than in mimids and in the following species of turdids: *Hylocichla mustelina* (Wood thrush), *Ixoreus naevius, Myadestes townsendi* (Townsend's solitaire), and all species of *Turdus*. It is larger and has a stouter Corpus humeri (shaft) than in *T. ustulatus* (Swainson's thrush). It is approximately equal in size to that of *C. fuscescens* (Veery), *C. minimus* (Gray-cheeked thrush), and the species of *Sialia* (bluebirds), but is told from these and all other Arizona turdids by having a relatively smaller Processus supracondylaris dorsalis, this being particularly evident in dorsal aspect, where P dorsalis is seen not to extend as far proximally in *C. guttatus* as in other species.

This is the first fossil record anywhere for *C. guttatus*. Brodkorb (1978) listed *C. guttatus* from the Late Pleistocene site of Carpinteria, California, citing A. H. Miller (1932*b*) as the authority. However, A. H. Miller (1932*b*) clearly did not refer the specimen in question, a humerus, to any species. Miller listed the specimen as "HYLOCICHLA? Thrush" (sic), stating that the fossil resembled *Hylocichla* (=*Catharus*) *guttata* in certain aspects, *H. mustelina* in others, and probably represented an extinct taxon of thrushes. The Hermit thrush is widespread in Arizona today, and is common in the Santa Catalina Mountains, nesting at high elevations and occurring elsewhere as a migrant or wintering bird.

Family Fringillidae—Sparrows, finches, tanagers, blackbirds, warblers, etc.
Subfamily Icterinae—Blackbirds, etc.
Genus and species indeterminate

Material.—Distal end of tarsometatarsus (15021).

Remarks.—This specimen is larger than the tarsometatarsus in all non-icterine, nine-primaried oscines of the Southwest. Among southwestern icterines, it is smaller than in *Sturnella magna* (Eastern meadowlark), *S. neglecta* (Western meadowlark), and *Cassadix mexicanus* (Boat-tailed grackle), and larger than in *Molothrus ater* (Brown-headed cowbird) or any species of *Icterus* (orioles). Of the species that it approximates in size, the fossil may be distinguished: from *Agelaius phoeniceus* (Red-winged black-

bird) and *Xanthocephalus xanthocephalus* (Yellow-headed blackbird) by its more dorso-plantar expansion of the middle and inner trochleae; from *Euphagus cyanocephalus* (Brewer's blackbird) and *E. carolinus* (Rusty blackbird) by its larger intertrochlear spaces, the more dorso-plantar expansion of the inner trochlea, and the more proximo-distally expanded outer trochlea; and from *Molothrus aeneus* (Bronzed cowbird) by its slightly wider outer intertrochlear space and slightly more laterally compressed inner trochlea. Overall, this specimen seems to be more similar to the tarsometatarsus of *Molothrus aeneus* than to any other living icterine, but is not similar enough to be referred confidently to that species.

The fossil icterine from Deadman Cave may represent an extinct taxon. Four species of extinct icterines have been described from rostra and mandibles from Late Pleistocene sites in North America. These are *Pandanaris convexa* (A. H. Miller 1947), and *Euphagus magnirostris* (A. H. Miller 1929), both from Rancho La Brea, California; *Pandanaris floridana* (Brodkorb 1957) from Reddick and Haile XIB, Florida; and *Pyeloramphus molothroides* (A. H. Miller 1932*a*) from Shelter Cave, New Mexico. Referred post-cranial elements have been reported for *Pandanaris floridana* and *Euphagus magnirostris,* but we have not examined this material. All Late Pleistocene icterines are in need of re-study (Steadman and Martin, in press), and pending such work the specimen from Deadman Cave is best left unidentified. Nevertheless, it may represent a new faunal element for Arizona.

Subfamily Emberizinae—"New World" sparrows, finches, etc.
Genus and species indeterminate

Material.—Tarsometatarsus lacking proximal end (15022).

Remarks.—Postcranial emberizine fossils are often very difficult or impossible to identify to genus or species. The present specimen is smaller than the tarsometatarsi of any icterine (blackbirds) or North American thraupine (tanagers), and is smaller than in most parulines (New World warblers). It differs from the tarsometatarsi of vireonids (vireos) in its more slender middle trochlea and broader inner trochlea, this last character also distinguishing it from the tarsometatarsi of parulines. Within the emberizines, no readily apparent patterns of tarsometatarsal variation are discernible. When compared to all species of North American emberizines, the fossil was found to be indistinguishable, both in size and quality, from the following species of medium-sized sparrows: *Ammodramus sandwichensis* (Savannah sparrow), *Melospiza lincolnii* (Lincoln's sparrow), *M. georgiana* (Swamp sparrow), *Junco hyemalis* (Dark-eyed junco), and *J. phaeonotus* (Mexican junco). Geographical and sexual variation combine to render the tarsometatarsus of these five species inseparable in many instances. Certain individuals of each species appear to be distinct, but no consistent variation is seen. Each of these species occurs today in southern Arizona, although in different habitats and in very different frequencies.

Class MAMMALIA—Mammals
Order INSECTIVORA—Insectivores
Family Soricidae—Shrews
Notiosorex crawfordi—Desert shrew

Material.—L mandible (3; 15023); R mandible (2; 15024).

Remarks.—The shape of the mandibles and the presence of three unicusps on each jaw were the identifying characters. *Notiosorex crawfordi* occurs fairly commonly as fossils in Arizona (Mead and Phillips 1981, Mead et al. 1983), New Mexico, and Texas (Harris 1977). Presently the Desert shrew occupies a wide variety of ecological situations from semi-desertscrub to woodland (Armstrong and Jones 1972). It is not known to occur at present in the Santa Catalina Mountains, but it does live nearby (Cockrum 1960).

Order CHIROPTERA—Bats
Family Vespertilionidae—Vespertilionid bats
cf. *Myotis*—Mouse-eared bat

Material.—L mandible with M_2 (15025); R mandible (3; 15027).

Remarks.—These specimens, clearly a vespertilionid based on the shape of the jaw, could not be identified unequivocally to genus because of fragmentation and/or for loss of teeth. Skinner (1942) reported *Myotis* cf. *M. velifer* (Cave myotis), *M.* cf. *M. thysanodes* (Fringed myotis), and *M.* cf. *M. evoltis* (Long-eared myotis) from Papago Springs Cave, Arizona.

Antrozous pallidus—Pallid bat

Material.—L femur (15025).

Remarks.—The greatest length of the fossil femur is 19.0 mm and the width of the proximal end is 3.0 mm (lesser trochanter to greater trochanter). A blade-like third trochanter is present. The Deadman Cave specimen was compared to *Myotis thysanodes, M. californicus* (California myotis), *M. velifer, Plecotus townsendii* (Townsend's big-eared bat), *Lasiurus borealis* (Red bat), *L. cinereus* (Hoary bat), *Macrotus waterhousei* (Leaf-nosed bat), *Tadarida brasiliensis* (Brazilian free-tailed bat), *T. femorosacca* (Pocketed free-tailed bat), *Mormoops megalophylla* (Ghost-faced bat), *Antrozous pallidus,* and *Eptesicus fuscus* (Big brown bat). Only the last two species were similar to the fossil in having a femur of total length averaging near 19.0 mm and a proximal width of 2.8 to 3.0 mm, along with the lesser trochanter as pronounced as the greater trochanter; but of these two, only *A. pallidus* had the third trochanter. The other species of bats lacked two or all of the criteria used to differentiate the fossil specimen.

The Pallid bat occurs throughout Arizona and can be found near Deadman Cave today (Cockrum 1960, Barbour and Davis 1969). Bats of the genus *Antrozous* have been recovered as fossils in a wood rat midden in the Sonoran Desert (Mead et al. 1983) and from Papago Springs Cave (Skinner 1942).

Order EDENTATA—Edentates
Family Megatheriidae—Megathere ground sloths
Nothrotheriops shastensis—Shasta ground sloth

Material.—Molar (15314).

Remarks.—Greg McDonald (Royal Ontario Museum, 1982, *personal communication*) confirmed this identification of *N. shastensis* and indicated that because the small molar contained a high percentage of hollow pulp cavity and lacked wear striations, it must have been from a fetal or new born sloth. Remains of the extinct Shasta ground sloth are very common in the Southwest, especially in Arizona (Long and Martin 1974, Thompson et al. 1980). A typographical error in Lindsay and Tessman (1974) has the sloth incorrectly located in Stanton's Cave, Grand Canyon.

Order LAGOMORPHA—Lagomorphs
Family Leporidae—Hares and rabbits
Sylvilagus species—Cottontail

Material.—L mandible; R mandibles (2); maxilla.

Remarks.—Postcranial remains of leporids were the second most common elements in the fossil deposit. The mandibles and the maxilla are not identified to species at this time because a more detailed study of all Late Pleistocene leporid remains of Arizona is in order and will be appearing in the near future (JIM). The genus is recovered from a number of Late Pleistocene localities in Arizona (Lindsay and Tessman 1974, Mead et al. 1983) and New Mexico (Harris 1977).

Lepus species—Jackrabbit

Material.—L mandibles (6); R mandibles (4); L maxillae (2); R maxillae (2); premaxilla; isolated molars (4); L femur proximal half.

Remarks.—See the remarks under *Sylvilagus. Lepus alleni* (Antelope jackrabbit) and *L. callotis* (White-sided jackrabbit) both presently occur in Arizona, but not near Deadman Cave. *L. californicus* occurs near Deadman Cave today. *Lepus californicus* (Black-tailed jackrabbit) was recovered from Papago Springs Cave (Skinner 1942) and other Arizona localities (Lindsay and Tessman 1974, Mead et al. 1983).

Order RODENTIA—Rodents
Family Sciuridae—Squirrels
Spermophilus variegatus—Rock squirrel

Material.—L mandible with M_{1-2} (2; 15028); R mandible (15029); L maxilla with M^{1-2} (15030).

Remarks.—*Spermophilus variegatus* can be differentiated from other species of ground squirrels by its larger size and the tendency of the skeleton to be slightly more rugose. The only other squirrel of similar size is *Sciurus aberti* (Abert's squirrel). The P^4 is relatively larger in *Spermophilus variegatus* as compared to that in *Sciurus.* The shape and medial inflection of the angle on the mandible is greater on *S. variegatus.* The Rock squirrel is a common ground squirrel and the largest within its distribution. It prefers rocky regions and is found throughout the Southwest, including the vicinity of Deadman Cave. Fossil remains of the Rock squirrel are not common in Late Pleistocene localities in the Southwest (Harris 1977, Mead 1981, Kurtén and Anderson 1980), although Skinner (1942) identified three mandibular rami of *S.* (=*Citellus*) *variegatus* from Papago Springs Cave.

Family Geomyidae—Pocket gophers
Thomomys cf. *T. bottae*—Bottae's pocket gopher

Material.—L & R maxillae (3; 15036); isolated teeth (9; 15037); R humerus (15038).

Remarks.—The upper incisors were lacking any conspicuous longitudinal groove, and the maxillary and isolated cheek teeth all were the lobbed, simple hypsodont molars and premolars of *Thomomys.* We follow Thaeler (1968) in using the designation *T. bottae,* which is the *T. umbrinus* of Hall (1981). The former species is common today in the Santa Catalina Mountains, and therefore, the reason for our identification of the fossils. The genus is a common fossil recovered in the Southwest (Mawby 1967, Lindsay and Tessman 1974, Harris 1977).

Family Heteromyidae—Pocket mice and Kangaroo rats
Perognathus cf. *P. flavus*—Silky pocket mouse

Material.—R maxillae (3; 15032); L maxillae (2; 15033); R mandibles (3; 15034); L mandibles (4; 15035).

Remarks.—The pocket mouse specimens from Deadman Cave compare well with *P. flavus,* although two other indistinguishable, small pocket mice, *P. parvus* (Great Basin pocket mouse) and *P. flavescens* (Plains pocket mouse) could also be in the assemblage. Our tentative identification is based on the present geographic distributions. Complete skulls are needed for unequivocal identification. *Perognathus flavus* lives near Deadman Cave region. The only other Late Pleistocene occurrence of this mouse is from Isleta Cave, New Mexico (Harris and Findley 1964).

Dipodomys spectabilis—Banner-tailed kangaroo rat

Material.—Bacculum (15031).

Remarks.—The shape of the bacculum of *Dipodomys spectabilis* is distinct from that of all other species. *Dipodomys spectabilis* is a large kangaroo rat that inhabits the

desert-grasslands of southeastern Arizona, including the valleys below the Santa Catalina Mountains (Cockrum 1960, Hall 1981). Harris (1977) has reported fossils of *D. spectabilis* from southern New Mexico.

Family Cricetidae—New World Rats and Mice

Reithrodontomys montanus—Plains harvest mouse

Material.—L mandible (15041); R mandibles (3; 15042).

Remarks.—The mandibles and teeth of the harvest mice from Deadman Cave compare favorably with those of *R. montanus.* The other harvest mice in Arizona, *R. megalotis* (Western harvest mouse) and *R. fulvescens* (Fulvous harvest mouse), are both larger than *R. montanus.* The occlusal pattern of the molar of *R. fulvescens* is an "S" configuration as opposed to a "C" in *R. montanus* (Hooper 1952).

Reithrodontomys montanus occurs today in the grasslands of southeastern Arizona but not in the Santa Catalina Mountains. The other two species occur in a wider variety of communities (Cockrum 1960). Fossil occurrences are discussed in Kurtén and Anderson (1980).

Peromyscus species—Deer mouse

Material.—L mandibles (4); R mandibles (4).

Remarks.—Fragments of *Peromyscus* can be confused with those of *Reithrodontomys.* The following characters will separate the two genera: 1) the M_3 is relatively larger on *Peromyscus,* 2) the articular condyle of the mandible extends more posteriorly than does the angle, on *Peromyscus,* and 3) the angle of the mandible has a less medial inflection on *Peromyscus.* We were unable to identify these specimens to species. Eight species of *Peromyscus* occur in southern Arizona, thus species level identification of fossils is extremely difficult if not impossible. Fossils of the genus have been recovered from all over the Southwest (Harris 1977, Kurtén and Anderson 1980, Mead et al. 1983).

Sigmodon species—Cotton rat

Material.—R mandible with M_{1-3} (15039); R maxilla with M^{1-2} (15040).

Remarks.—The occlusal pattern on all cheek teeth are distinct in *Sigmodon.* We are not able to identify our specimens to species. Four species of cotton rat now inhabit southern Arizona (Hall 1981). *Sigmodon hispidus* (Hispid cotton rat) occurs on the western and eastern borders of southern Arizona while *Sigmodon arizonae* (Arizona cotton rat) lives in the area of the Santa Catalina Mountains. Both *S. fulviventer* (Tawny-bellied cotton rat) and *S. ochrognathus* (Yellow-nosed cotton rat) occur south and east of Deadman Cave (Baker and Shump 1978*a, b,* Hall 1981). *S. ochrognathus* was recovered from a wood rat midden near the Santa Catalina Mountains (Mead et al. 1983). The genus has a rich fossil record throughout the Southwest (Lindsay and Tessman 1974, Harris 1977).

Neotoma albigula—White-throated wood rat

Material.—L mandibles (3); R mandibles (4); L maxillae (3); R maxillae (7); LM_1 (7); RM_1 (8); LM^1 (11); RM^1 (15); M^2_2 (55); M^3_3 (15).

Remarks.—All the *Neotoma* remains compare well with *N. albigula.* The occlusal patterns for adult teeth are well-rounded as in *N. albigula* and *N. lepida* (Desert wood rat), but the teeth are much larger than those of modern *N. lepida.* The anterolingual re-entrant on the M_1 are very shallow as in *N. albigula* compared to the deep, microtine-like dental characters of *N. mexicana* (Mexican wood rat).

Five species of *Neotoma* presently live in Arizona (Colorado Plateau), more than in any other state. Only *N. lepida, N. albigula,* and *N. mexicana* inhabit southern Arizona today, and only the last two presently occur in the vicinity of Deadman Cave. *N. albigula* lives in desert-grassland and desertscrub habitats while *N. mexicana* occurs

TABLE 2. Measurements of modern and fossil dentaries (Deadman and Rampart caves) of *Bassariscus astutus*. Measurements are rounded to the nearest 0.5 mm.

	n	OR	$\bar{x}$
	Alveolar length P_4–M_1		
Deadman Cave	1	24.0	24.0
Modern Arizona	13	21.0–23.0	22.0
Rampart Cave, Arizona (northern)	1	27.9	27.9
	Alveolar length M_1		
Deadman Cave	1	8.0	8.0
Modern Arizona	13	6.5–7.5	7.0
Rampart Cave, Arizona (northern)	1	6.5	6.5

in higher woodland and forest areas. *Neotoma stephensi* (Stephen's wood rat) occurs in the northern half of the state and *N. cinerea* (Bushy-tailed wood rat) in the northeastern sector (Cockrum 1982). The midden of the wood rat is found in numerous dry localities throughout the Southwest and is radiocarbon dated back to more than 40 000 B.P. (Van Devender 1977, Van Devender and Spaulding 1979).

Microtus species—Meadow vole

Material.—L mandible (15043); LM_1 (2: 15044); RM_1 (15045); RM^3 (3: 15046).

Remarks.—We have not identified the fossil teeth to the specific level. We find it difficult to differentiate *M. longicaudus* (Long-tailed vole) from *M. montanus* (Montane vole) using isolated molars. Of the three complete fossil M_1s examined, two had four closed alternating triangles and one had five triangles.

None of the four species of vole found in Arizona presently occur near Deadman Cave. *Microtus mexicanus* (Mexican vole) presently occurs in the mountainous region of eastern Arizona but may have had a wider, more western distribution, based upon the present isolated occurrence of *M. m. hualpaiensis* in northwestern Arizona, in the Late Pleistocene and/or Early Holocene (Hall 1981). The Mexican vole was also identified in the fossil remains from Papago Springs Cave (Skinner 1942). *Microtus montanus* (Montane vole) has a predominantly northwestern distribution in the United States. Its nearest occurrence to Deadman Cave is in the Arizona Strip region of northernmost Arizona and in east-central Arizona. *Microtus pennsylvanicus* (Meadow vole) lives mainly in northern and eastern North America but approaches Arizona in northwestern New Mexico. The Meadow vole may have had a more southern, mountainous distribution in the Late Pleistocene or Early Holocene based upon an isolated modern population in northwestern Chihuahua, Mexico (Bradley and Cockrum 1968). *Microtus longicaudus* occurs through much of western North America, including northeastern Arizona. An isolated population presently lives in the Pinaleño Mountains only 60 km east of Deadman Cave. Based on present geographic distributions, this species seems most likely to have inhabited the mountains of the Basin-and-Range province of southeastern Arizona during the Late Pleistocene and Early Holocene.

Order CARNIVORA—Carnivores
Family Procyonidae—Racoons, coatis, and ringtails
Bassariscus astutus—Ringtail

Material.—R mandible P_{2-3} (15062); R maxilla (15315); LP^4 (15316).

Remarks.—The fossil Ringtail specimen compares well with modern specimens except that the M_2 is not developed in the fossil specimen, but is replaced by a distinct depressional scar where the tooth was to have developed. The alveolar length from P_4 to M_1 (Table 2) is slightly longer in the Deadman Cave specimen than in modern specimens. The mandible from Deadman Cave does not seem to be similar to the rami

TABLE 3. Measurements of dentaries (modern and Deadman Cave) of *Spilogale putorius*. Measurements are rounded to nearest 0.5 mm.

	n	OR	$\bar{x}$
	Alveolar length P_2–M_2		
Deadman Cave	5	15.5–18.0	16.5
Modern Arizona	7	12.5–14.5	13.5
Modern Nevada (northern)	1	15.8	15.8
	Alveolar length P^2–M^1		
Deadman Cave	1	14.0	14.0
Modern Arizona	8	11.5–13.0	12.5
Modern Nevada (northern)	1	12.0	12.0

described as *B. sonoitensis* from Papago Springs Cave (Skinner 1942). Late Pleistocene and Holocene localities of the Ringtail are shown in Mead and Van Devender (1981).

The Ringtail is widespread in rocky habitats in the desert grassland, and woodlands of the Southwest, and lives today in Deadman Cave. Numerous modern scats are located throughout the cave, especially near the entrance as demonstrated by the accumulations of seeds, insects, and bones.

Family Mustelidae—Weasels, skunks, and badgers

Spilogale putorius—Spotted skunk

Material.—L mandibles (3; 15047–15049); R mandibles (6; 15050–15055); L maxilla (15056); R maxillae (2; 15057–15058); L humerus (15059).

Remarks.—The specimens from Deadman Cave are consistently larger than modern specimens of *S. putorius* (Table 3). The Spotted skunk is common throughout the Southwest and can be found in the Santa Catalina Mountains down to the lower desert mountain ranges. Elsewhere, fossil remains of the Spotted skunk have been recovered from Arizona (Skinner 1942), California (Stock 1930), and New Mexico (Harris 1977).

Mephitis macroura—Hooded skunk

Material.—L mandibles (2; 15060); L maxilla (15061); L humerus (15317).

Remarks.—The left mandible compares most favorably with that of *Mephitis macroura,* being smaller than in *M. mephitis* (Striped skunk) or *Conepatus mesoleucus* (Hog-nosed skunk) yet definitely larger than in *Spilogale.* All three skunks occur in southern Arizona, including the Santa Catalina Mountains. *Mephitis macroura* has its present northern distribution in southern Arizona and New Mexico (Hall 1981). We know of no other Late Pleistocene–Early Holocene record of this taxon.

Family Felidae—Cats

Felis concolor—Mountain lion

Material.—LC^1 (15063); LC_1 (15064); RC_1 (15065).

Remarks.—All the canines compared well with *F. concolor* rather than *Panthera leo atrox* (American lion) which has been recovered from Late Pleistocene age deposits of the nearby Murray Springs site (Haynes 1968, J. J. Saunders *personal communication*). The canines were compared in size to those of modern Arizona Mountain lions and fossil specimens from Rancho La Brea, California, El Durado, Colorado, Tule Springs, Nevada (Kurtén 1973), and Rampart Cave, Arizona (Table 4). There were no discernible differences other than that the Late Pleistocene *Felis concolor* canines from Rancho La Brea may have been slightly larger than those from Deadman Cave.

The Mountain lion occurs historically and paleontologically throughout the Southwest, including the Santa Catalina Mountains (Hall 1981). Although it is usually found in woodlands and forest country, it also lives in rugged ranges well within the Sonoran Desert.

TABLE 4. Length (L; anterior–posterior) and breadth (B; labial–lingual) range of measurements of canines in modern and Late Pleistocene–Early Holocene Mountain lion (*Felis concolor*). Recent specimens from Arizona (44, 654, 22785, and 23444; Department of Ecology and Evolutionary Biology, University of Arizona, Tucson). Measurements (in millimeters) of fossil specimens, other than from Deadman and Rampart caves, from Kurtén (1976).

		C^1		C_1	
	n =	L	B	L	B
Recent Arizona	4	10.9–13.2	9.4–11.9	10.8–13.2	8.0–9.8
Deadman Cave, Arizona	3	11.3	10.3	11.0–11.3	8.2–8.6
Rampart Cave, Arizona	1	12.8	9.9	—	—
Rancho La Brea, California	3	—	—	12.4–16.4	11.2–12.5
El Dorado, Colorado	2	12.6	11.0	12.0	9.8
Tule Springs, Nevada	1	—	9.8	—	—

Order PERISSODACTYLA—Odd-toed ungulates
Family Equidae—Horses
Equus species—Horse

Material.—2nd phalanx (15027).

Remarks.—This single element of a horse could not be identified to species. Remains of extinct species of Horse are common throughout the Southwest (Stock 1930, Mawby 1967, Lindsay and Tessman 1974, Harris 1977, Harris and Porter 1980, Kurtén and Anderson 1980). Skinner (1942) identified *E. conversidens* and *E. tau* from Papago Springs Cave.

Order ARTIODACTYLA—Even-toed ungulates
Family Cervidae—Cervids
Odocoileus species—Deer

Material.—LP_2 (15066).

Remarks.—The Deadman Cave specimen of *Odocoileus* could not be identified to species. Today in southern Arizona *O. hemionus* (Black-tailed deer) lives in the lowland habitats while *O. virginiana* (White-tailed deer) is found on the mountain tops. Fossil remains of both species of deer are widespread in North America (Kurtén and Anderson 1980), although only a few Late Pleistocene localities in Arizona contain remains of deer (Lindsay and Tessman 1974, Mead 1981).

Family Bovidae—Bovids
Euceratherium collinum—Shrub-ox

Material.—L mandible (15318).

Remarks.—The single specimen of the extinct Shrub-ox was identified by Walter Dalquest and Ernest Lundelius (Dalquest 1981, *personal communication*). The occlusal surface of the teeth were very worn, indicating an old individual. This specimen is the first record of the Shrub-ox in Arizona. Kurtén and Anderson (1980) describe this bovid as a large, specialized grazer that probably lived in the lower foothills (like at Deadman Cave) rather than in the high, forested mountains. *Euceratherium collinum* is also known from Burnet Cave, New Mexico (Schultz and Howard 1935), but is not a common component of Late Pleistocene faunas in the Southwest (Kurtén and Anderson 1980).

DISCUSSION

Localities

Although there are numerous Late Pleistocene age localities in Arizona, especially in the southern portion (Lindsay and Tessman 1974), most of these sites are isolated

finds in alluvial deposits containing *Mammuthus jeffersoni* (Jefferson's mammoth; =*M. columbi, fide* Kurtén and Anderson 1980), *Camelops* species (camel), *Equus* species, or *Bison* species (bison).

The most current work in Arizona concerning Late Pleistocene (Wisconsinan) age deposits comes from the well-preserved, radiocarbon dated wood rat middens, but these localities rarely contain the larger animals (Van Devender and Mead 1978, Mead 1981, Mead et al. 1983). The only cave faunas studied in southern Arizona are Papago Springs Cave (Skinner 1942) and Ventana Cave (Haury 1950). Ventana Cave (145 km west of Deadman Cave, Fig. 1) was excavated primarily for its abundant archaeological remains. Two lower units, Volcanic and Conglomerate, were deposited during the Wisconsinan glacial episode (Haury 1950). Papago Springs Cave (112 km south of Deadman Cave, Fig. 1) was excavated solely for its Late Pleistocene vertebrate fossils, which were laborously chiseled from brecciated layers along the walls and ceiling of the cave (Skinner 1942).

The two cave faunas are very different in composition (Table 1). The fourteen taxa recovered from the lower units in Ventana Cave were all mammals, whereas a bird and 32 mammals were recovered from Papago Springs Cave. Only *Canis latrans* (=*C. caneloensis*; Coyote), *Lepus californicus,* and *Taxidea taxus* (Badger) are shared in both faunas. Of the 64 taxa from Deadman Cave (5 amphibians, 25 reptiles, 12 birds, and 22 mammals), only *Nothrotheriops shastensis* is shared with Ventana Cave and five species (*Spermophilus variegatus, Thomomys* cf. *T. bottae, Neotoma albigula, Antrozous pallidus,* and *Spilogale putorius*) are shared with Papago Springs Cave. Each cave is in a different physiographic setting in southern Arizona and had different modes of fossil accumulation. Deadman Cave is a limestone cave on a large mountain mass between two major river valleys surrounded by Sonoran and Chihuahuan desertscrub communities; its fauna was collected predominantly by small carnivores and raptors. Ventana Cave is a volcanic rockshelter in a small, low-elevation desert mountain range presently surrounded by the hot, dry Sonoran Desert. The open cave provided some shelter, easy access, as well as water from a spring. Papago Springs Cave was an open limestone cave in rolling oak woodland in the Canelo Hills of southeastern Arizona.

The Late Wisconsinan age assignment of the deposition of the Volcanic and Conglomerate units in Ventana Cave is presumably correct (Haury 1950, *see* Long and Muller 1981). The fossils from Papago Springs Cave are only broadly assigned to the Late Pleistocene, but for several reasons we suggest that the Papago Springs Cave deposit was formed prior to the last glacial maximum in the Wisconsinan (>22 000 B.P.). The chamber within the cave has changed configuration greatly since the initial deposition of the fauna. A great abundance of rock rubble (10 m thick) with bones has filled the cavern and become cemented. According to Skinner (1942) the cave was sealed off from the outside for a period of time, allowing settling and cementing of the fossils to take place. A third stage in the history of the cave reopened the cavern entrances permitting recent faunal accumulations and partial erosion of the fossil deposits. We feel that such an accumulation may have required a few ten's of thousands of years, placing the time of deposition sometime in the Middle or Early Wisconsinan glacial episode.

Fauna

Five species of amphibians (all anurans) were identified from Deadman Cave (Table 1). Of these, only *Bufo punctatus* and *Scaphiopus couchi* were reported prior to this report from the Late Pleistocene and Early Holocene of Arizona. We report *Bufo* cf. *B. woodhousei, Scaphiopus* cf. *S. hammondi,* and *Rana* sp. for the first time as fossils in Arizona, although they have been previously recorded from Late Pleistocene localities in California, Nevada, and New Mexico. Except for *B. woodhousei,* all anurans from the Deadman Cave fauna are found nearby the cave today.

Reptiles are better known than the amphibians from Late Pleistocene–Early Holocene deposits in Arizona. We report 25 reptiles, including 13 species of lizards and 12 species of snakes, from Deadman Cave. Of the lizards, *Callisaurus draconoides,*

Holbrookia maculata, H. texana, Phrynosoma douglassi, P. modestum, P. solare, Sceloporus cf. *S. clarkii,* and *Urosaurus ornatus* have not been reported previously from the Late Pleistocene of Arizona. The records of *Heloderma suspectum* from Vulture Cave, Arizona, and Gypsum Cave, Nevada, may be Early or Middle Holocene in age, and therefore this species perhaps should be added to the above list. Most of these lizards have previous fossil records from sites in California, Nevada, and/or New Mexico. *Callisaurus draconoides* is reported for the first time as a Late Wisconsinan–Early Holocene fossil. *Phrynosoma modestum* and *C. draconoides* do not presently inhabit the region of Deadman Cave nor the immediate valley. The closest occurrence of *P. modestum* is in Chihuahuan desert-grassland 95 km east of the cave. *Callisaurus draconoides* occurs just west of Deadman Cave in lower Sonoran desertscrub. The other lizards from Deadman Cave, as well as most of the snakes, now live within a raptor's hunting range of the fossil locality. Of the 12 species of snakes identified from Deadman Cave, only *Gyalopium canum* has not been previously reported as a fossil from Arizona, and is out of its present distributional range at Deadman Cave.

The birds from Deadman Cave represent only the fifth Late Pleistocene avifauna to be reported from Arizona. This contrasts markedly with the adjacent states of New Mexico and California, each of which has an excellent record of Late Pleistocene birds. The Deadman Cave avifauna is especially significant in that the diverse Sonoran Desert avifauna has yielded very few Pleistocene fossils.

The Deadman Cave fauna contains several new avian fossil records, none of which is unexpected. *Micrathene whitneyi* and *Catharus guttatus* are reported for the first time as fossils, while *Cyrtonyx montezumae* is recorded paleontologically for the first time anywhere in the United States. New Arizonan fossil records include *Colinus gambelli, Colinus* species, *Zenaida* cf. *Z. macroura, Otus* species, *Asio otus,* the indeterminate caprimulgid, icterine, and *Colaptes auratus.*

Mammals are the best known group of fossil vertebrates from Arizona. Twenty-two mammals are identified from Deadman Cave, most of which can be found in the Santa Catalina Mountains today or in the surrounding valleys. Exceptions are the three large extinct species (*Equus* species, *Nothrotheriops shastensis,* and *Euceratherium collinum*) and *Microtus* species which lives 60 km to the east of Deadman Cave.

Paleoenvironment of Deadman Cave

The amphibian remains indicate that the region around Deadman Cave was at least as moist at the time of deposition as it is today. Certainly pools of water were nearby as they are today in portions of the Santa Catalina Mountains and along the major streams and rivers. The lizard fossils argue for either a community that was a composite of today's vegetational communities, or, a few vegetation groups abutting each other in close proximity to the cave. The presence of *Phrynosoma modestum* suggests that a desert-grassland area may have occurred on the broad flat hills above the large river valley, at the base of the mountain mass. *Callisaurus draconoides, Holbrookia texana, Sceloporus magister,* and *Heloderma suspectum* indicate a more-or-less open desertscrub to desert-grassland. Such areas could easily abut an open woodland. This community would probably be in the lower part of the bajadas between hills. The rest of the lizard fauna indicates several vegetation communities ranging from desert and desert-grassland to woodland. Certainly some areas of talus or rock outcrops were nearby. Most of the snake population from Deadman Cave suggests little to distinguish the region then from what it is today, although *Gyalopium canum* indicates a cool grassland habitat.

Except for the possibly extinct icterid, the entire avifauna of Deadman Cave consists of living taxa that occur today in southern Arizona. No birds in the fauna are restricted to coniferous habitats. In fact, *Colinus gambelli* and *Micranthene whitneyi* argue strongly against any sort of adjacent coniferous forest. *Colinus gambelii* suggests the presence of desertscrub, while *Cyrtonyx montezumae* is characteristic of open oak woodlands, and pine-oak woodlands. *Cyrtonyx* is the only bird from Deadman Cave

that is not found at least occasionally in desertscrub today, although *Turdus migratorius* and *Catharus guttatus* are certainly more abundant in wooded areas than in desertscrub, and never nest in the latter. The fossil birds from Deadman Cave suggest a slightly more grassy and wooded condition in the Latest Pleistocene and Earliest Holocene than today, such as an evergreen oak grassland mixed with desertscrub and desert-grassland on the more xeric exposures, and oak woodland on more protected, mesic areas.

The mammals generally indicate an open woodland with some areas more vegetated and other areas more xeric and open. None of the mammals are restricted to forested habitats, although many of them do occur today in the forested higher elevations of nearby larger mountains. *Notiosorex crawfordi, Microtus* sp., *Reithrodontomys montanus,* and *Euceratherium collinum* may argue for an open, possibly grassy woodland. Today this sort of habitat occurs just a few hundred meters upslope from Deadman Cave. *Perognathus* cf. *P. flavus, Dipodomys spectabilis, Thomomys* cf. *T. bottae,* and *Sigmodon* cf. *S. arizonae* indicate that a desertscrub to desert-grassland was nearby.

No distinctly boreal or mesic mammals (e.g., *Sorex ornatus,* Ornate shrew; *S. palustrus,* Water shrew; *Ochotona princeps,* Pika; *Marmota flaviventris,* Yellow-bellied marmot; *Glaucomys sabrinus,* Northern flying squirrel) were recovered from Deadman Cave. This may be because the faunal assemblage is of Late Wisconsinan–Early Holocene transition in age, and the boreal-mesic (full glacial) elements had already become extirpated locally. This may be the case with the *Spermophilus lateralis* from Ventana Cave. An alternative is that most of these elements never did occur in southern Arizona during the last Wisconsinan full and late glacial (assuming that the Papago Spring Cave deposit is Middle Wisconsinan or older in age). Presumably if any geographically or ecologically extralocal small animals, such as listed above, were contemporaneous with the Shasta ground sloth, Horse, and Shrub-ox, they too would have been observed in the Deadman Cave deposit.

The Deadman Cave faunal record is very similar to those of Early Holocene–Late Pleistocene wood rat faunas in the Sonoran Desert (Van Devender and Mead 1978, Mead et al. 1983) and Grand Canyon (Van Devender et al. 1977, Mead and Phillips 1981) in that the small vertebrates were conservative with few animals out of their present range, although there was a greater change in the local vegetation. The pollen record at Willcox Playa, 80 km east of the Santa Catalina Mountains, recorded a pine forest at 1200 m elevation 20 000 years ago in an area that now supports desert-grassland (Martin 1963). This is an estimated lowering of the vegetation zones by about 1000 m elevation. The wood rat midden record for lower areas in the Sonoran Desert in southwestern Arizona recorded a complex elevational lowering of 600 m or less of certain woodland plants into the desert. An equivalent lowering of vegetation zones in the Santa Catalina Mountains would imply a shift from the modern desert-grassland-oak woodland vegetation to Pondersoa pine mixed conifer forest or a Mexican pine-oak woodland, depending on the distribution and abundance of precipitation in the Late Wisconsinan (Whittaker and Niering 1968). In the Early Holocene a Mexican pine-oak woodland was probably near the site until about 8000 years ago with the grassland developing more recently. Like the *Microtus* sp., a population of *Abies lasiocarpa* (Corkbark fir) presently on the top of the Santa Catalina Mountains, is also isolated from its nearest population in the spruce forests of the Pinaleño Mountains. Most of the remaining Deadman Cave fauna would be found in some sort of open woodland today. Several animals including *Callisaurus draconoides, Heloderma suspectum, Dipodomys spectabilis, Phrynosoma modestum,* and *Colinus gambelli* do not live in Mexican pine-oak woodland today and are more likely to occur in open desert-grassland or desertscrub and may represent the Early Holocene portion of the Deadman Cave deposit. Another possibility which has been demonstrated for a few animals in the Sonoran Desert (Van Devender and Mead 1978; Mead et al. 1983) is that under an equable Late Wisconsinan climate certain animals now confined to deserts were able to live in more diverse woodland communities.

Conclusions

The vertebrate fauna of Deadman Cave includes 5 amphibians, 25 reptiles (13 lizards and 12 snakes), 12 birds, and 22 mammals for a total of 64 species. The implication from this faunal assemblage is that by the end of the late glacial and the beginning of the post glacial (8000–12 000 B.P.), most of the local fauna was essentially as it is today—modern. Only one amphibian (*Bufo woodhousei*), three reptiles (*Callisaurus draconoides, Phrynosoma modestum, Gyalopium canum*), and one mammal (*Microtus* species) are locally extirpated, although all still occur in southern Arizona. Animals unequivocally extinct are the Shrub-ox, Horse, and Shasta ground sloth, all large mammals. An unidentified icterine bird may prove to be an extinct species. Overall, the Deadman Cave fauna suggests that the vegetation community of the Late Pleistocene and Early Holocene were rather similar to those found today in the same region.

The Deadman Cave bone assemblage has expanded our knowledge of the Late Pleistocene–Early Holocene fauna of southern Arizona, and has provided new questions on Late Pleistocene zoogeography of the hot deserts. Further stratified and datable cave deposits and wood rat middens need to be studied to refine when the faunas of southern Arizona became "modern." Upland localities need to be studied to determine whether boreal and/or mesic faunal elements ever existed in the Late Wisconsinan of southern Arizona, and whether the presently extralocal and local faunal assemblages ever coexisted.

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Literature Cited

Armstrong, David M., and J. Knox Jones, Jr. 1972. *Notiosorex crawfordi*. Mammalian Species No. 17.

Auffenberg, W. 1963. The fossil snakes of Florida. Tulane Studies in Zoology 10:131–216.

Baker, Rollin H., and Karl A. Shump, Jr. 1978*a*. *Sigmodon fulviventer*. Mammalian Species No. 94.

———, and ———. 1978*b*. *Sigmodon ochrognathus*. Mammalian Species No. 97.

Barbour, Roger W., and Wayne H. Davis. 1969. Bats of America. University Press of Kentucky, USA.

Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breasile, and H. E. Evans. 1979. *Nomina Anatomica Avium*. Academic Press, London.

Bradley, W. Glen, and E. Lendell Cockrum. 1968. A new subspecies of the meadow vole (*Microtus pennsylvanicus*) from northewestern Chihuahua, Mexico. American Museum Novitates No. 2325.

Brattstrom, B. H. 1953*a*. The amphibians and

reptiles from Rancho La Brea. Transactions of the San Diego Society of Natural History 11: 365–392.

———. 1953*b*. Records of Pleistocene reptiles from California. Copeia 1953:174–179.

———. 1954*a*. Amphibians and reptiles from Gypsum Cave, Nevada. Bulletin of the Southern California Academy of Science 53:8–12.

———. 1954*b*. The fossil pit-vipers (Reptilia: Crotalidae) of North America. Transactions of the San Diego Society of Natural History 12(3): 31–46.

———. 1964*a*. Amphibians and reptiles from cave deposits in south-central New Mexico. Bulletin of the Southern California Academy of Science 63:93–103.

———. 1964*b*. Evolution of the pit vipers. Transactions of the San Diego Society of Natural History 13(11):185–268.

———. 1976. A Pleistocene herpetofauna from Smith Creek Cave, Nevada. Southern California Academy of Science Bulletin 75:283–284.

Brodkorb, Pierce. 1957. New passerine birds from the Pleistocene of Reddick, Florida. Journal of Paleontology 31:129–138.

———. 1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). Bulletin of the Florida State Museum, Biological Series 8:195–335.

———. 1978. Catalogue of fossil birds, Part 5 Bulletin of the Florida State Museum, Biological Series 23:139–228.

Cockrum, E. Lendell. 1960. The recent mammals of Arizona. University of Arizona Press, Tucson, USA.

———. 1982. Mammals of the Southwest. University of Arizona Press, Tucson, USA.

Cole, Kenneth L., and Jim I. Mead. 1981. Late Quaternary animal remains from packrat middens in the eastern Grand Canyon, Arizona. Journal of the Arizona-Nevada Academy of Science 16:24–25.

Gehlbach, Frederick R., and J. Alan Holman. 1974. Paleoecology of amphibians and reptiles from Pratt Cave, Guadalupe Mountains National Park, Texas. Southwestern Naturalist 19:191–198.

Hall, E. Raymond. 1981. The mammals of North America. John Wiley and Sons, New York, USA.

Harris, Arthur H. 1977. Wisconsin age environments in the northern Chihuahuan Desert: evidence from the higher vertebrates. Pp. 23–51 *in* Roland H. Wauer and David H. Riskind (eds.). Transactions of the symposium on the biological resources of the Chihuahuan Desert region United States and Mexico. National Park Service Transactions and Proceedings Series No. 3.

———, and James S. Findley. 1964. Pleistocene-Recent fauna of the Isleta Caves, Bernalillo County, New Mexico. American Journal of Science 262:114–120.

———, and Linda S. W. Porter. 1980. Late Pleistocene horses of Dry Cave, Eddy County, New Mexico. Journal of Mammalogy 61:46–65.

Haury, Emil W. 1950. The stratigraphy and archaeology of Ventana Cave. The University of Arizona Press, Tucson, USA.

Haynes, C. Vance. 1968. Preliminary report on the late Quaternary geology of the San Pedro Valley, Arizona. Arizona Geological Society, Southern Arizona Guidebook III:79–96.

Hill, William H. 1971. Pleistocene snakes from a cave in Kendall County, Texas. Texas Journal of Science 22:209–216.

Holman, J. Alan. 1962. A Texas Pleistocene herpetofauna. Copeia 1962:255–261.

———. 1970. A Pleistocene herpetofauna from Eddy County, New Mexico. Texas Journal of Science 22:29–39.

Hooper, Emmet T. 1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Miscellaneous Publications of the Museum of Zoology, University of Michigan No. 77.

Howard, Hildegarde. 1963. Fossil birds from the Anza-Borrego Desert. Los Angele County Museum of Natural History, Contributions to Science No. 73.

———, and A. H. Miller. 1933. Bird remains from cave deposits in New Mexico. Condor 35:15–18.

Hudson, Dennis M., and Bayard H. Brattstrom. 1977. A small herpetofauna from the late Pleistocene of Newport Beach Mesa, Orange County, California. Bulletin of the Southern California Academy of Science 76:16–20.

Jones, J. Knoxes, Jr., Dilford C. Carter, Hugh H. Genoways, Robert S. Hoffmann, and Dale W. Rice. 1982. Revised checklist of North American Mammals north of Mexico, 1982. Occasional Papers the Museum Texas Tech University 80:1–20.

Kurtén, Bjorn. 1976. Fossil puma (Mammalia: Felidae) in North America. Netherlands Journal of Zoology 26:502–534.

———, and Elaine Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.

Lindsay, Everett H., and Norman T. Tessman. 1974. Cenozoic vertebrate localities and faunas in Arizona. Journal of the Arizona Academy of Science 9:3–24.

Long, Austin, and Paul S. Martin. 1974. Death of American ground sloths. Science 186:638–640.

———, and A. B. Muller. 1981. Arizona radiocarbon dates X. Radiocarbon 23:191–217.

Lowe, Charles H. 1964. The vertebrates of Arizona. University of Arizona Press, Tucson, USA.

Martin, Paul S. 1963. Geochronology of pluvial Lake Cochise, southern Arizona, II pollen analysis of a 42-meter core. Ecology 44:436–444.

———. 1967. Prehistoric overkill. Pp. 75–120 *in* Paul S. Martin and Herbert E. Wright (eds.). Pleistocene extinctions, the search for a cause. Yale University Press, New Haven, Connecticut.

Mawby, John E. 1967. Fossil vertebrates of the Tule Springs site, Nevada. Pp. 105–128 *in* H. M. Wormington and Dorothy Ellis (eds.). Pleistocene Studies in Southern Nevada. Ne-

vada State Museum, Anthropological Papers 13.

Mead, Jim I. 1981. The last 30,000 years of faunal history within the Grand Canyon, Arizona. Quaternary Research 15:311–326.

———, and Arthur M. Phillips, III. 1981. The late Pleistocene and Holocene fauna and flora of Vulture Cave, Grand Canyon, Arizona. Southwestern Naturalist 26:257–288.

———, and Thomas R. Van Devender. 1981. Late Holocene diet of *Bassariscus astutus* in the Grand Canyon, Arizona. Journal of Mammalogy 62:439–442.

———, Robert S. Thompson, and Thomas R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake Range, Nevada. Transactions of the San Diego Society of Natural History 20:1–26.

———, Thomas R. Van Devender, and Kenneth L. Cole. 1983. Late Quaternary small mammals from Sonora Desert packrat middens, Arizona and California. Journal of Mammalogy 64:173–180.

Meltzer, David J., and Jim I. Mead. 1983. The timing of late Pleistocene mammalian extinctions in North America. Quaternary Research 19:130–135.

Miller, A. H. 1929. The passerine remains from Rancho La Brea in the paleontological collections of the University of California. University of California Publication, Bulletin of the Department of Geological Sciences 19:1–22.

———. 1932*a*. An extinct icterid from Shelter Cave, New Mexico. Auk 49:38–41.

———. 1932*b*. The fossil passerine birds from the Pleistocene of Carpinteria, California. University of California Publication, Bulletin of the Department of Geological Sciences 21:169–194.

———. 1947. A new genus of icterid from Rancho La Brea. Condor 49:22–24.

———. 1943. The Pleistocene birds of San Josecito Cavern, Mexico. University of California Publication in Zoology 47:143–168.

Montanucci, R. R., R. W. Axtell, and H. C. Dessauer. 1975. Evolutionary divergence among collared lizards (*Crotaphytus*) with comments on the status of *Gambelia*. Herpetologica 31: 336–347.

Mosimann, James E., and Paul S. Martin. 1975. Simulating overkill by Paleoindians. American Scientist 63:304–313.

Phillips, A., J. Marshall, and G. Monson. 1964. The Birds of Arizona. University of Arizona Press, Tucson, USA.

Rea, Amadeo M. 1980. Late Pleistocene and Holocene turkeys in the Southwest. Contributions to Science of the Natural History Museum of Los Angeles County 330:209–224.

———, and Lyndon L. Hargrave. In Press. Bird bones from Stanton's Cave, Arizona.

Reeve, W. L. 1952. Taxonomy and distribution of the horned lizard genus *Phrynosoma*. University of Kansas, Science Bulletin 34(14):817–915.

Schultz, B. C., and E. B. Howard. 1935. The fauna of Burnet Cave, Guadalupe Mountains, New Mexico. Proceedings of the Philadelphia Academy of Natural Science 87:273–298.

Skinner, Morris F. 1942. The fauna of Papago Springs Cave, Arizona and the Study of *Stockoceros*: with three new antilocaprines from Nebraska and Arizona. Bulletin of the American Museum of Natural History 80:143–220.

Smith, N. M., and W. W. Tanner. 1972. Two new subspecies of *Crotaphytus* (Sauria: Iguanidae). Great Basin Naturalist 32:25–34.

Stebbins, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston, USA.

Stock, Chester. 1930. Rancho La Brea. Los Angeles County Museum of Natural History, Science Series No. 20.

Thaeler, Charles S. 1980. Chromosome numbers and systematic relations in the genus *Thomomys* (Rodentia: Geomyidae). Journal of Mammalogy 61:414–422.

Thompson, Robert S., Thomas R. Van Devender, Paul S. Martin, Theresa Foppe, and Austin Long. 1980. Shasta ground sloth (*Nothrotheriops shatense* Hoffstetter) at Shelter Cave, New Mexico: environment, diet and extinction. Quaternary Research 14:360–376.

Van Devender, Thomas R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Ph.D. Dissertation. University of Arizona, Tucson.

———. 1977. Holocene woodlands in the southwestern deserts. Science 198:189–192.

———, and Richard D. Worthington. 1977. The herpetofauna of Howell's Ridge Cave and the paleoecology of the northwestern Chihuahuan Desert. Pp. 85–106 *in* Roland H. Wauer and David H. Riskind (eds.). Transactions of the symposium on the biological resources of the Chihuahuan Desert region United States and Mexico. National Park Service Transactions and Proceedings Series No. 3.

———, and Jim I. Mead. 1978. Early Holocene and late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. Copeia 1978:464–475.

———, and W. Geoffrey Spaulding. 1979. Development of vegetation and climate in the Southwestern United States. Science 204:701–710.

———, Amadeo M. Rea, and Michael L. Smith. In Press. An interglacial vertebrate fauna from Rancho La Brisca, Sonora, Mexico. Transactions of the San Diego Society of Natural History.

———, Arthur M. Phillips, III, and Jim I. Mead. 1977. Late Pleistocene reptiles and small mammals from the Lower Grand Canyon of Arizona. Southwestern Naturalist 22:49–66.

Wallace, Robert M. 1955. Structures at the northern end of the Santa Catalina Mountains, Arizona. Unpublished Ph.D. Dissertation. University of Arizona, Tucson.

Whittaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains: a gradient analysis of the south slope. Ecology 46: 429–452.

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A Pliocene Flora from Chula Vista, San Diego County, California

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Abstract. A small fossil flora from the marine Upper Pliocene San Diego Formation suggests that the adjacent coastal plain was then covered with an avocado–Monterey pine–live oak woodland associated with palm, cottonwood, willow, and sycamore along streams. Fossil digger pine apparently was confined to drier, warmer sites away from the coast. At higher, cooler levels farther inland were stands of fossil Jeffrey pine. Precipitation was near 50–58 cm over the lowlands, increasing to about 65 cm in stands of fossil Jeffrey pine near 450–600 m. The fossil avocado, palm, and pine (aff. *Pinus radiata* var. *binata*) indicate summer rainfall, consistent with the Late Pliocene higher-than-present sea surface temperature. Mean annual temperature on the coast was approximately 16°C, and annual range was about 7–8°C, equability was near *M* 70 with frost absent along the coast, light in the interior.

Comparison with Pliocene floras in northern California shows that the Chula Vista flora lived in a separate floristic province, one corresponding with cismontane southern California which has been a distinct floristic province since at least the Middle Miocene. Two new species of fossil pine are described: *Pinus diegensis* new species (allied with the living *P. radiata* var. *binata*) and *P. jeffreyoides* new species (similar to the living *P. jeffreyi*).

The Chula Vista flora provides new evidence regarding the evolutionary history of *Pinus radiata* populations, and further insight into the disjunct distribution of taxa in the montane conifer forests of southern California and Baja California.

Introduction

The recent discovery of a small flora of Late Pliocene age (ca. 3 m.y.) at Chula Vista, in southwestern San Diego County, California (Fig. 1), provides preliminary information on the late Tertiary flora, vegetation, and climate of the region. The flora lived at a critical time in Neogene environmental history, one characterized by the cooler, moister climate that followed the warm, dry episode of the latest Miocene (5–6 m.y.) (Axelrod 1980*b*). The climatic transition, which heralds the build-up of ice sheets in Alaska and border areas, resulted in the displacement southward of relatively xeric sclerophyllous vegetation with numerous Madrean taxa, and their replacement by a more mesic flora. The nearest floras of comparable age are in central and northern California (Fig. 2). Analysis of the Chula Vista flora thus provides a general, though tentative, basis for interpreting the regional floristic differences that arose as cooler, moister climate spread southward and into lower altitudes in the Late Pliocene.

Geology

The geology of the classical marine Pliocene San Diego Formation at San Diego has been summarized recently (Deméré 1983). This rock unit crops out over a broad area which includes much of the southwestern portion of San Diego County, and the extreme northwestern corner of Baja California, Mexico. The San Diego Formation

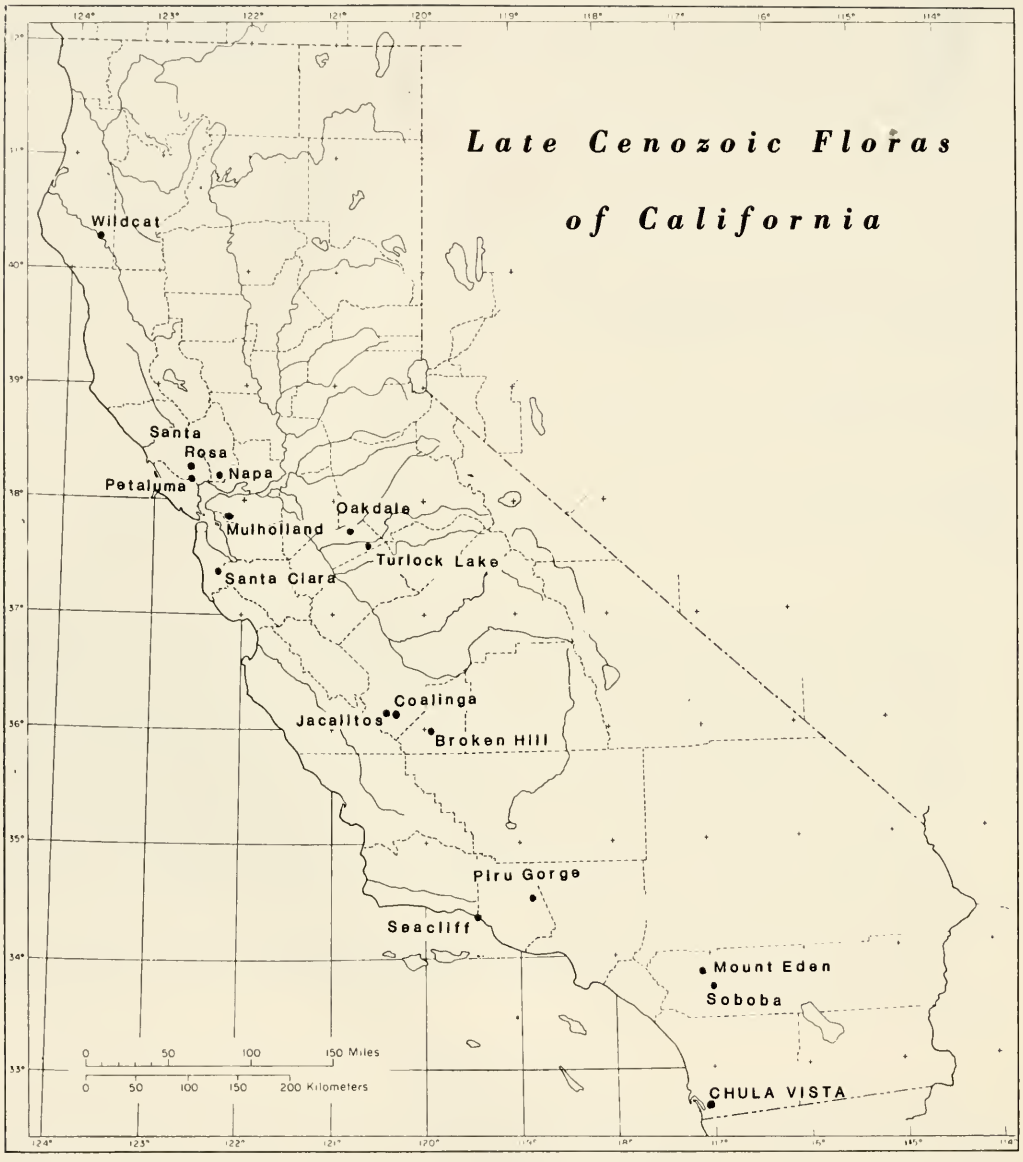

FIGURE 1. Late Cenozoic floras to which reference is made.

was deposited during a marine transgression of the Neogene San Diego Basin, which like other onshore sedimentary basins in southern California (e.g., Ventura Basin, Los Angeles Basin) is structurally related to the wrench and extensional tectonics of the continental borderland. Deposition began during the Late Pliocene and apparently continued into Early Pleistocene time, accumulating at least 75 m of marine and 9 m of nonmarine sedimentary rocks. The overall stratigraphic sequence suggests a successive shallowing and filling of this basin. It is now apparent that extensional tectonics have controlled both the initial deposition as well as the present outcrop distribution of this rock unit. Numerous high-angle normal faults striking north to northwest cut the area into a series of small fault blocks which expose different portions of the Pliocene section.

In an attempt to correlate between the fault blocks, Deméré (1983) informally subdivided the San Diego Formation into a "lower" and an "upper" member using

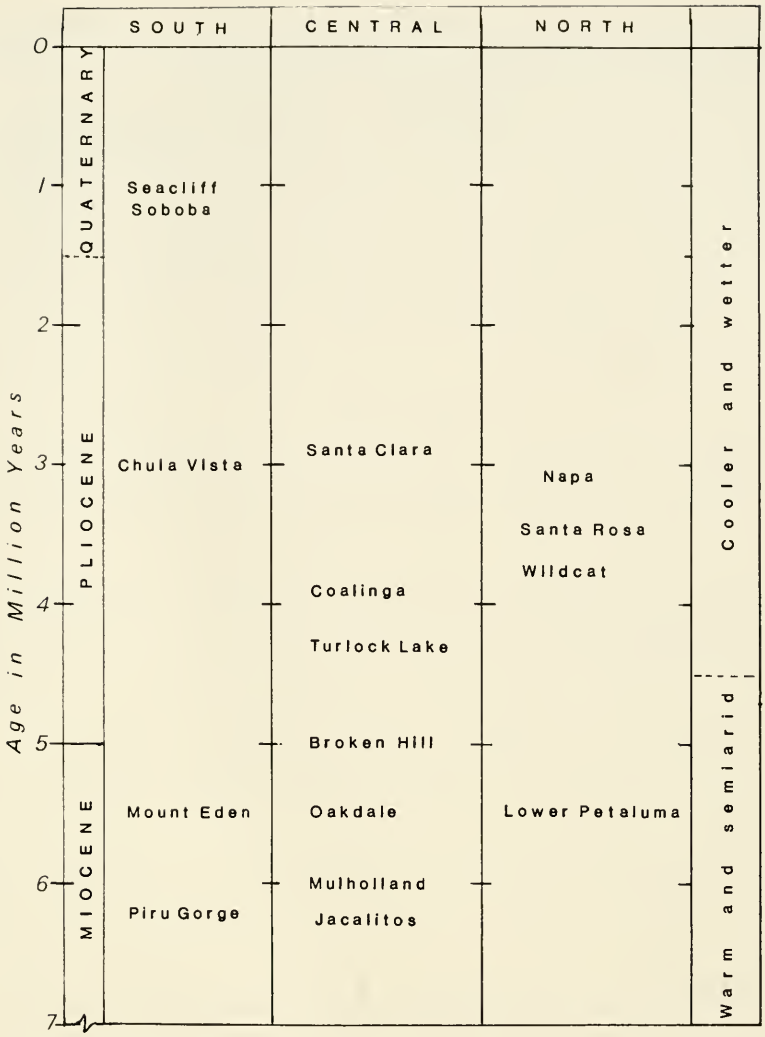

FIGURE 2. Ages of Late Cenozoic floras in California.

both lithologic and paleontologic criteria. The "lower" member is characterized by yellowish, very fine-grained, micaceous, massive, friable sandstones with locally well-bedded sequences of laminated and cross-bedded sandstones, pebble-to-cobble conglomerates and well-cemented shell beds. This "lower" member is richly fossiliferous and has produced the bulk of the marine invertebrate fauna so well known through the work of Grant and Gale (1931) and Hertlein and Grant (1944, 1960, 1972). In addition, the diverse avifauna (Howard 1949, Miller 1956) and cetacean assemblage (Barnes 1973, 1976) reported from the San Diego Formation have been largely collected from the "lower" member.

Lithologically the "upper" member is characterized by well-bedded sequences of pebble-to-cobble conglomerate containing reworked "Poway" clasts, well-cemented fossiliferous sandstones, and medium- to coarse-grained friable sandstones. Marine invertebrate fossils are locally common in this member.

In terms of paleoenvironment, the "lower" member contains a middle-to-outer-shelf molluscan fauna characterized by *Patinopecten healeyi, Pecten stearnsii, Lucinoma annulata* and *Opalia varicostata*. In contrast, molluscs from the "upper" member indicate deposition in littoral-to-inner-shelf depths. Characteristic species include *Pec-*

ten bellus, Argopecten hakei, Nucella lamellosa and *Dendraster ashleyi*. Both members reflect normal marine deposition in a broad coastal embayment probably similar to present-day Monterey Bay along the central California coast.

Barnes (1976) correlated the San Diego Formation ("lower" member) with the Blancan North American land mammal stage. This was based on the occurrence of the horse *Equus*, and is supported by the recent discovery at Chula Vista of teeth referable to the bunodont mastodon (*Stegomastodon rexroadensis* Woodburne). Relying on the stratigraphic ranges of molluscan species the "lower" member is correlative with the upper portion of the San Joaquin Formation in the San Joaquin Basin, the Careaga Formation in the Santa Maria Basin, and the Niguel Formation and the upper Fernando Formation in the southeastern Los Angeles Basin, all Late Pliocene in age (Woodring and Bramlette 1951, Vedder 1972). In turn the "upper" member of the San Diego Formation is correlated with the lower Santa Barbara Formation in the Ventura Basin which is considered to be Late Pliocene to Early Pleistocene in age (Keen and Bentson 1944, Lajoie et al. 1982). The meager microfossil record available in the San Diego Formation (Ingle 1967, Mandel 1973) suggests that it is apparently no older than planktonic foraminiferal zone N-21 (approximately 3.0 million years B.P. Late Pliocene) and is perhaps as young as the *Emiliania annula* calcareous nannoplankton subzone (approximately 1.5 million years B.P., Early Pleistocene).

The section at Chula Vista consists of approximately 73 m of fossiliferous San Diego Formation. Here the Pliocene marine rocks rest disconformably on fluvial and lacustrine sedimentary rocks of the Middle Miocene Sweetwater Formation. Overlying the San Diego Formation along an irregular erosion surface are fluvial and alluvial sedimentary rocks of the Lower Pleistocene Sweitzer Formation (=Lindavista Formation of Kennedy 1975). The lower 46 m of the Chula Vista Pliocene section contain marine invertebrate taxa characteristic of the "lower" member of the San Diego Formation. This part of the section is also characterized by locally common marine vertebrate fossils and has produced all of the paleobotanical material described in this report.

In terms of general stratigraphic position, the described fossil pine cones were found betwen 24 and 30 m above the base of the San Diego Formation, the fossil leaves between 12 and 19 m, and a few poorly preserved shipworm (*Teredo*)-bored logs between 12 and 21 m.

The fragmentary cones occur in large, elongate (up to 40 cm in diameter), limy concretions which formed around large bones of fossil baleen whales. Steinkerns of marine invertebrates also occur in these concretions. The cones are preserved as natural internal and external molds and vary from incomplete three-dimensional specimens to only partial imprints.

Fossil leaves occur as dense concentrations of flat-lying and stacked leaf material in both fine-grained sandstone and sandy siltstone. The leaves are preserved as iron-stained imprints and are largely fragmentary. The leaves were collected from thin (15 cm thick) sandstone and siltstone strata interbedded with fossiliferous sandstones containing typical "lower" San Diego Formation marine invertebrate taxa (e.g., *Patinopecten healeyi* and *Lucinoma annulata*). The occurrence of terrestrial plant material in this marine setting points to offshore transport, no doubt first under fluvial and then under marine conditions. The concentration of leaf material in thin stratigraphic horizons suggests marine transport by storm-generated debris flows. Otherwise, it seems doubtful that they would be concentrated in a local area. The cones probably were transported in a similar manner. The cone fragments are the result of partial preservation in the concretions, the remaining portion of the cone was not preserved in the soft compacted sandstones that enclose the concretions.

Not described in this report, but occurring within the Pliocene section at Chula Vista, were a number of severely shipworm-bored, calcareously cemented logs. Some of these logs were up to 3 m in length and had broken branch stems. They all were lying parallel to the bedding upon locally pebbly fossiliferous sandstone.

TABLE 1. Systematic list of floral species from the San Diego Formation, Chula Vista, California.

Pinaceae	Salicaceae
Pinus diegensis n. sp.	*Populus alexanderi* Dorf
Pinus jeffreyoides n. sp.	*Salix wildcatensis* Axelrod
Pinus pieperi Dorf	Fagaceae
Arecaceae	*Quercus lakevillensis* Dorf
Gen. et sp. indet. (Palm)	Lauraceae
Juncaceae	*Persea coalingensis* (Dorf) Axelrod
Gen. et sp. indet. (Reed)	Platanaceae
	Platanus paucidentata Dorf

COMPOSITION

The small paleobotanical collection from Chula Vista includes ten species distributed among three conifers, two monocotyledons, and five dicotyledons. Two of the pines are new. The monocotyledons are represented by specimens too incomplete to refer to species.

The fossil taxa are represented by only a few specimens each, and most are fragmentary, reflecting their transport into the offshore. Fifteen specimens are referred to *Persea*. Of the remainder, *Pinus diegensis* is represented by 5 specimens, *Populus* 4, *Platanus, Salix, Pinus jeffreyoides* 3 each, and *Pinus pieperi,* palm, *Quercus* and reed by one each.

All of the fossils are similar to living taxa and have been assigned to fossil species following nomenclatural convention (Axelrod, 1980*b*:205). As judged from their relationships, the flora is composed of 8 trees, one shrub and one herbaceous perennial.

An understanding of the ecology of extant species closely allied to the fossil plants in the Chula Vista flora provides a basis for reconstructing the paleovegetation and climate of the region. These allied modern species can be separated into four ecologic and geographic groups.

First, several of the allied living species are widely distributed in central and southern California. These include sycamore (*Platanus*), cottonwood (*Populus*) and willow (*Salix*). Today, these trees inhabit streambanks in the coastal area from near San Francisco Bay southward, reaching also into the interior. The oak (*Quercus agrifolia*) forms dense woodlands in moister, more equable sites near the coast and contributes to open oak-grass communities at low to moderate elevations in more inland areas of the outer Coast Ranges. *Quercus* is also found frequently along stream margins where it is associated with cottonwood, sycamore, and willow. The fossil cottonwood (*Populus alexanderi*) is similar to *P. trichocarpa* var. *trichocarpa* that has roundish-ovate leaves and lives near the coast in mild equable climate from the San Francisco Bay region southward. It differs from the black cottonwood that occurs in the mountains of California and northward, which has larger, ellipitic-ovate leaves and is best referred to *P. hastata* Dode.

Second, digger pine (*Pinus sabiniana*) characterizes the pine–oak woodland–grass vegetation of the inner Coast Ranges and lower slopes of the Sierra Nevada. It reaches the margin of southern California in Santa Ynez Valley north of Santa Barbara and on Liebre Mountain several miles southeast of Tejon Pass. It only approaches the coast in the Santa Lucia Mountains near Gorda where it seems to be a relict of the Xerothermic period. This also appears to account for its disjunct occurrence in Santa Ynez Valley. In the south Coast Ranges it inhabits flats adjacent to rivers, notably the Salinas, Santa Maria, Santa Ynez, and Sisquoc, which at times of flood probably transport its large cones to the coast. Among its associates in riparian sites are species of cottonwood, willow, sycamore, and live oak similar to taxa in the Chula Vista flora.

Third, *Pinus jeffreyi,* allied to the fossil *P. jeffreyoides* new species, now occurs in

FIGURE 3. Guadalupe Island pine (*Pinus radiata* var. *binata*) and palm (*Brahea edulis*) on Guadalupe Island have allied taxa in the Chula Vista fossil flora. (Photo by Reid Moran.)

the mountains of eastern San Diego County. The stand nearest to Chula Vista is 55 km northeast at Pine Valley, at an elevation of 1050 m. There it is associated with live oak (*Quercus agrifolia*). Streams in the area also support species of willow, cottonwood and sycamore similar to those in the fossil flora. The bordering slopes are covered with dense chaparral composed of *Adenostoma, Arctostaphylos, Ceanothus, Cercocarpus, Quercus,* and others. It is to be noted that *P. jeffreyi* replaces *P. ponderosa* as the lowest montane conifer forest species in the southern Peninsular Ranges. Here it is a distinct ecotype as compared with *P. jeffreyi* in the Sierra Nevada which is a member of the red fir–white pine–mountain hemlock forest that is snowbound all winter. Only an occasional light snow occurs at its lower elevations in San Diego County and in the Sierra Juarez and Sierra San Pedro Martir, northern Baja California, where it also meets oak woodland and chaparral vegetation, generally at levels near 1400–1500 m (see Nelson 1922).

Fourth, three Chula Vista fossil species are allied to living taxa in western Mexico. Avocado (*Persea*), which was abundant in California into the close of the Tertiary (Sonoma, Wildcat, Turlock Lake, Broken Hill, Coalinga floras), now occurs from southern Sonora southward in the Sierra Madre Occidental, and other species are in the eastern United States, chiefly along the Atlantic seaboard. In southern Sonora and Sinaloa, *Persea* is a frequent member of pine–oak woodland vegetation, associated with sycamore, willow, palm and other riparian taxa in valley bottoms. It occupies sheltered sites at 1000–1200 m under mild, equable climate (Gentry 1942, 1946).

Cones of *Pinus diegensis* new species are similar to those of *P. radiata* var. *binata* of Guadalupe Island, situated 350 km off the central coast of Baja California at 29°N latitude. This pine is confined chiefly to the middle–upper slopes of the island, generally at altitudes above 800 m where it is in a persistent fog belt during summer. The occurrence of *P. diegensis* on the mainland as recently as 3 m.y. ago suggests that the living *P. radiata* var. *binata* did not originate in insular isolation but probably was confined to Guadalupe Island as drier climate spread over the region.

A fragmentary specimen of palm frond from Chula Vista shows relationship to

FIGURE 4. Present environment in the area of the Chula Vista fossil flora.

Sabal and also to *Brahea* (=*Erythea*). *Sabal* is a frequent member of the pine–oak woodland in the Sierra Madre Occidental of Sonora where it occurs along streams with avocado, willow, sycamore and other riparian inhabitants. Of considerable interest is the presence of *Brahea edulis* H. Wendl. ex. S. Wats. on Guadalupe Island where it occurs in deep, moist canyons with *Pinus radiata* var. *binata* (Howell 1941*b*; Libby et al. 1968), as seen in Fig. 3.

VEGETATION

The community relations of modern species most similar to the fossil plants suggest that during the Late Pliocene this portion of the coastal strip was covered with dense woodland vegetation in contrast to the open coastal sage of today (Fig. 4). The abundance of avocado leaves in the collection implies that *Persea* dominated stream valleys and sheltered slopes near the shore. On moister slopes it was associated with fossil Guadalupe pine and probably formed a dense forest. Live oak was regularly associated with the pine and avocado. Along stream borders these trees occurred with sycamore, cottonwood, willow, and palm. Toward the interior, fossil Guadalupe pine (*P. diegensis*) and live oak probably contributed to a more open woodland–grass community that gradually merged with a fossil digger pine association that included avocado and palm in sheltered sites, as well as riparian taxa. Fossil digger pine probably attained optimum development on exposed, hotter and drier south-facing slopes provided by granitic and metamorphic basement rocks farther inland. At higher, cooler and moister levels farther east were stands of fossil Jeffrey pine that reached down to a lower altitude than at present because precipitation was higher.

CLIMATE

Judging from conditions under which allied living taxa occur, annual precipitation at sea level during the Late Pliocene probably was near 58–63 cm as compared with

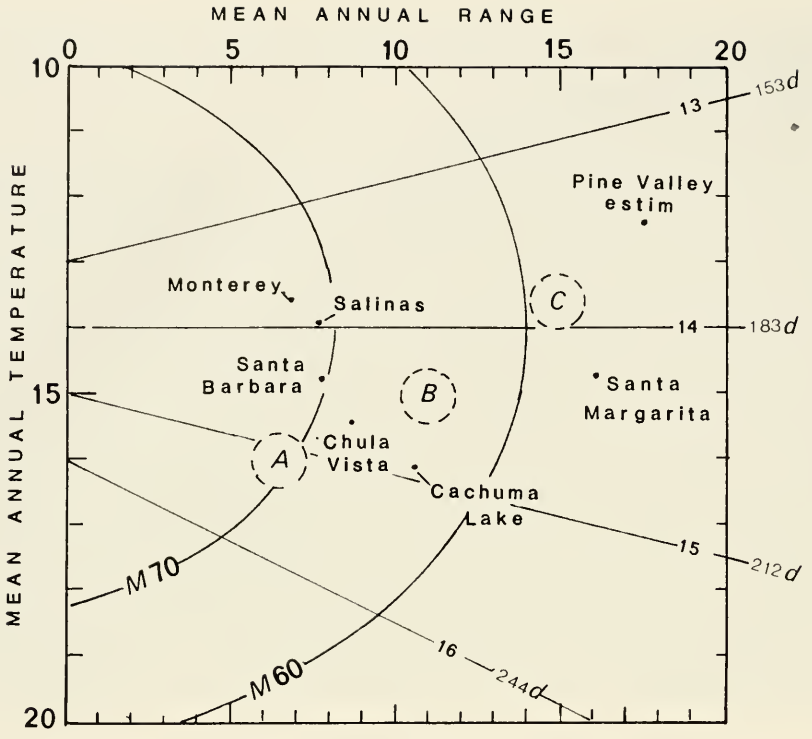

FIGURE 5. Estimated paleotemperature for the Chula Vista coastal strip (A), the area of fossil digger pine (B), and the fossil Jeffrey pine forest (C). The difference in mean annual temperature between Chula Vista today and the inferred paleotemperature (circled area, A) is approximately 0.5°C. The radiating lines of warmth (*W*) indicate growing seasons defined by the number of days (*d*) with mean temperature warmer than the specified temperature (i.e., *W* 14°C has 183 days with mean temperature warmer than 14°C). The arcs *M* 70 and *M* 60 represent a measure of equability which decreases in all directions from *T* 14°C and *A* 0°C. For further data see Bailey (1960, 1964).

22 cm at Chula Vista today. Precipitation increased to about 70 cm in hills to the east at the lower margin of fossil Jeffrey pine forest. The remaining taxa in the fossil flora could readily survive under these rainfall totals. Fossil avocado, palm and Guadalupe pine (var. *binata*) indicate summer rainfall. This resulted from a warmer sea-surface temperature than that of today, as shown by the marine macro-invertebrate fauna of the San Diego Formation. Hertlein and Grant (1954) estimated on the basis of the molluscan taxa that *winter* sea surface temperature during the Late Pliocene was similar to that now near Cedros Island (ca. 17–18°C), or fully 3–4°C higher than that in the San Diego area today (U.S. Navy 1956–58; U.S. Weather Bureau 1938). With warmer water, hurricanes from the eastern Pacific may have moved farther up the coast than they now do. In this regard, the summer of 1983 in southern California was characterized by warmer-than-usual water offshore and increased warm season rainfall onshore.

Because of the mixture of taxa from both coastal and inland sites, a single estimate cannot represent the thermal conditions for the entire fossil flora. As for the coastal strip, Guadalupe pine occurs at altitudes generally above 800 m. To judge from its occurrence in a summer fog belt, mean annual temperature is approximately 16°C as inferred from sea surface temperature (U.S.D.A., Climatic data); the persistent fog belt implies a low range of temperature, probably not more than 8–10°C. Because the marine invertebrate fauna of the "lower" San Diego Formation indicates that sea surface temperature was warmer than at present, temperature along the coastal plain was also warmer than at present, probably with a mean temperature near 16°C. This is suggested also by the abundance of avocado (*Persea*) specimens. Since avocado does not now

produce fruit well in areas much north of Santa Barbara (Fig. 5), temperatures near there probably represent an extreme minimum for the fossil flora. Digger pine occurs today in Santa Ynez Valley (Cachuma Lake), not far from avocado groves, where mean temperature is about 16°C and the range is 10–11°C. Farther north in the Coast Ranges, as at Santa Margarita (alt. 300 m), mean annual temperature is 14.5°C and the annual range is 16°C. The palm, Guadalupe pine, and avocado suggest that fossil digger pine lived under conditions milder than those now at Santa Margarita, and probably were like those in the Cachuma Lake area. As for the interior, Jeffrey pine now occurs in Pine Valley where mean annual temperature, as estimated from that at Cuyamaca, 16 km north and 350 m higher, is near 12.5°C and the mean monthly range is about 17°C. These estimates suggest that during the Late Pliocene the temperature along the coast was about 0.5–1.0°C warmer than that presently at Chula Vista.

In view of the greater range of mean monthly temperature in the interior where fossil Jeffrey pine lived, mean annual temperature there probably was about 2–2.5°C lower than on the coast (Fig. 5). This suggests a depression of regional climate of about 300–400 m, and hence a lower altitude for taxa representing upland vegetation as compared with their present occurrence. Coupled with higher rainfall, under the postulated paleotemperature fossil Jeffrey pine may have reached down to near 600 m as compared with 1050 m in Pine Valley today. Fossil Jeffrey pine would therefore have lived closer to the marine embayment, in sites from which its cones would more likely be transported seaward, especially during floods resulting from hurricanes that presumably were of more frequent occurrence. As suggested in Fig. 5, equability on the coast was near *M* 70 as compared with *M* 67 at Chula Vista today. Frost was absent on the coast where the growing season probably had a mean daily temperature warmer than 15.2°C on 218 days of the year. Moderate light frosts might well be expected over the interior where fossil Jeffrey pine lived. The estimated paleotemperatures are shown by the circled areas A, B, and C, respectively, for the immediate coast, the central digger pine woodland, and the lower margin of Jeffrey pine forest (Fig. 5).

Regional Comparisons

Pliocene Floras

The coastal oak–avocado–palm–pine woodland, the interior digger pine–oak woodland and the upland Jeffrey pine forest of the Pliocene Chula Vista flora differ considerably from contemporaneous vegetation in central and northern California (Fig. 1).

The flora from the Sonoma Formation at Neer's Hill, Santa Rosa (Axelrod 1944*c*) represents a coast conifer forest with redwood (*Sequoia*), lowland fir (*Abies* cf. *grandis*), Douglas fir (*Pseudotsuga* cf. *menziesii*), coast hemlock (*Tsuga* cf. *heterophylla*) and winged seeds of weeping spruce (*Picea* cf. *breweriana*). Associated with the conifers, and also forming a dense, broadleaved sclerophyll forest on warmer slopes, were species of oak (*Quercus* cf. *chrysolepis*), chinquapin (*Castanopsis* [*Chrysolepis*] *chrysophylla*), California laurel (*Umbellularia*), and tanoak (*Lithocarpus*). Riparian species included sycamore, cottonwood, avocado, and willow. A few Tertiary relicts are recorded, notably species of *Ilex, Persea, Trapa* and *Ulmus*. It is estimated that the area received fully 89–100 cm of rainfall, some in summer, and that temperatures were cool though frost was absent.

Representatives of the Sonoma flora apparently extended farther north, as suggested by a small flora from the upper part of the Wildcat Group near Garberville (Axelrod 1944*c*:187, Dorf 1930). This fossil flora is composed chiefly of riparian taxa and is characterized by an absence of typical forest species. The flora apparently accumulated on a broad floodplain some distance from forests that occupied slopes bordering the lowland marine basin. The only forest representatives are logs of *Sequoia* and *Pseudotsuga* and a leaf of *Ulmus*. Members of floodplain vegetation included alders (*Alnus* cf. *rhombifolia, rubra*), avocado (*Persea* cf. *borbonia*), sycamore (*Platanus* cf. *racemosa*), black cottonwood (*Populus* cf. *hastata*), willow (*Salix* cf. *lasiolepis*) and California laurel (*Umbellularia*). Some of these appear to represent Miocene relicts, notably the

TABLE 2. Comparison of Chula Vista flora with related living taxa.

Fossil species	Allied living species
Pinus diegensis	*P. radiata* var. *binata* Englemann
Pinus jeffreyoides	*P. jeffreyi* Murray
Pinus pieperi	*P. sabiniana* Douglas
Platanus paucidentata	*P. racemosa* Nuttall
Populus alexanderi	*P. trichocarpa* Torrey & Gray
Persea coalingensis	*P. podadenia* Blake; *P. borbonia* (Linne) Sprengel
Quercus lakevillensis	*Q. agrifolia* Nee
Arecaceae sp.	*Brahea*?, *Sabal*?
Shrub	
Salix wildcatensis	*S. lasiolepis* Bentham
Herbaceous perennial	
Juncaceae sp.	*Juncus*?

Persea, Populus, Ulmus and possibly the *Platanus* which is represented by an incomplete specimen. Their persistence here in the late Tertiary is understandable in view of their coastal position where there was high rainfall and low evaporation. It is evident that the Garberville flora shows little relation to the Chula Vista flora which is expectable in view of its position fully 1025 km southeast.

The Napa flora (Axelrod 1950*a*), situated 45 km southeast of the Sonoma flora at Santa Rosa, represents a pine (*Pinus* cf. *ponderosa*)–Douglas fir (*Pseudotsuga*) forest living near sea level. Forest associates included chinquapin (*Castanopsis* [*Chrysolepis*] cf. *chrysophylla, C. sempervirens*), Oregon grape (*Mahonia* cf. *nervosa*), ocean spray (*Holodiscus* cf. *discolor*), goldcup oak (*Quercus chrysolepis*), interior liveoak (*Q.* cf. *wislizenii*), and California laurel (*Umbellularia* cf. *californica*). *Sequoia* is rare, with only three small twigs represented in the sample of over 700 specimens. Warmer slopes were covered with broadleaved sclerophyll vegetation composed of *Castanopsis, Quercus, Umbellularia,* and probably *Persea.* An open oak woodland–grass of coast liveoak (*Quercus* cf. *agrifolia*), valley oak (*Q. lobata*), and interior liveoak (*Q. wislizenii*) occupied drier slopes. The warmer, driest sites supported a chaparral of whitehorn (*Ceanothus* cf. *leucodermis*), mountain mahogany (*Cerocarpus* cf. *betuloides, C.* cf. *ledifolius*), and toyon (*Heteromeles* cf. *arbutifolia*), though these shrubs also occurred in the oak woodland. Stream- and lake-border sites supported avocado (*Persea*), sycamore (*Platanus*), willows (*Salix* cf. *laevigata, S. scouleriana*) and California laurel (*Umbellularia*). The assemblage reflects a drier, more continental climate than that in the Santa Rosa area to the northwest. The only relationship with the Chula Vista flora is seen in a few riparian taxa that ranged widely and through several vegetation zones.

The Turlock Lake flora, slightly older than the Chula Vista, accumulated on the lowest floodplain in front of the central Sierra Nevada. It is preserved in the upper part of the Mehrten Formation 35 km east of Modesto (Axelrod 1980*b*). The lake border assemblage included avocado (*Persea*), sycamore (*Platanus*), paloblanco (*Forestiera*), willow (*Salix*), and California laurel (*Umbellularia*). The bordering slopes were covered with oak woodland–grass (*Quercus* cf. *douglasii, Q. wislizenii*) and scattered shrubs, including scrub oaks (*Quercus* cf. *dumosa, Q. dunnii*), ceanothus (*Ceanothus* cf. *sorediatus*), coffeeberries (*Rhamnus californica, R. ilicifolia*), and poison oak (*Toxicodendron*) that may have formed local brushy patches on exposed drier slopes. Cooler, moister sites supported broadleaved sclerophyll taxa, notably madrone (*Arbutus*), interior live oak (*Q. wislizenii*), and California laurel (*Umbellularia*). Reaching down from higher levels along stream valleys were members of a moister flora, including pine (*Pinus* cf. *ponderosa*) and smilax (*Smilax* cf. *californica*). Two exotics are in the flora, an aspen (*Populus* cf. *tremula*) and a cherry (*Prunus*), both of Asian affinity. There was some summer rainfall and annual precipitation totalled approximately 63

cm as compared with 36 cm today. The flora shows little relationship with that at Chula Vista apart from several widely distributed riparian species.

The small Coalinga flora from the upper San Joaquin Formation 10 km south of Coalinga indicates that the same general type of floodplain vegetation preserved at Turlock Lake ranged across the Central Valley. The fossils occur in sandstones of fluviatile origin interbedded with marine strata containing molluscs that represent the *Pecten coalingensis* zone (Dorf 1930). The flora has abundant leaves of avocado (*Persea*) and sycamore (*Platanus*), and together with cottonwood (*Populus*) and hackberry (*Celtis*) are indicative of riverbanks and moist sites. Adjacent interfluves were covered with oak (*Quercus* cf. *douglasii*) as well as silk-tassel bush (*Garrya* cf. *elliptica*). Further collecting at this site should provide a better representation of the flora and vegetation of this area.

An indication of the flora that occupied the region slightly earlier (ca. 5 m.y.) is provided by a flora from Broken Hill, 30 km southeast, at the south end of North Dome, Kettleman Hills, in the basal part of the San Joaquin Formation (Axelrod 1980*b*). It also provides evidence of vegetation in the area prior to uplift of the Coast Ranges directly west, an event that brought a drier, semidesert climate to this area. The flora occurs in sandstones of fluviatile origin that grade upward into marine beds. Floodplain vegetation included alder (*Alnus*), sycamore (*Platanus*), cottonwood (*Populus*), poplar (*Populus euphratica*), aspen (*Populus* cf. *tremula*), California laurel (*Umbellularia*) as well as several willows (*Salix* cf. *exigua, S. lasiandra, S. laevigata, S. lasiolepis*), and soapberry (*Sapindus*). Avocado (*Persea*) is abundant, magnolia is present, and both contributed to the floodplain vegetation. Well-drained interfluves were covered with oak woodland–grass that included three oaks (*Quercus* cf. *agrifolia, Q. douglasii, Q. wislizenii*). There is also evidence of broadleaved sclerophyll vegetation, probably on higher slopes to the west. These included tanoak (*Lithocarpus*), morheus oak (*Q. morheus*), and California laurel (*Umbellularia*), as well as avocado and magnolia. The flora has several exotics in addition to *Magnolia* and *Persea,* notably *Populus* cf. *tremula, P.* cf. *euphratica, Sapindus* and *Ulmus,* all indicating summer rainfall. Apart from these, the flora resembles vegetation of the lower middle slopes of the Santa Lucia Mountains 120 km west. Rainfall is estimated to have been near 75 cm annually, and climate was more equable than that now in this semi-desert region where precipitation totals 12 cm yearly.

Evidently the Pliocene floras of central and northern California represent vegetation quite different than that at Chula Vista. Much as the vegetation of these areas differs today, the differences reflect the uniqueness of the floristic provinces represented. The principal links with the floras to the north were riparian taxa that ranged widely into very different vegetation zones and which have a broad time span. The transition from the northern coast conifer forests to the coastal vegetation of the Chula Vista area probably corresponded generally with the axis of the present Transverse Ranges.

Plio-Pleistocene

The preceding late Neogene floras were succeeded by those that represent colder, moister climates. This is illustrated by the Soboba flora from interior southern California (Axelrod 1967*a*), dated by the Bautista mammalian fauna at 1 m.y. This flora shows that mixed conifer forest reached down fully 1000 m below its present level in the San Jacinto Mountains which now tower above the fossil locality. Included as macrofossils that represent montane conifer forest are *Abies concolor, Calocedrus decurrens, Pinus ponderosa, P. lambertiana,* and *Populus tremuloides.* Associates included species of upper woodland and chaparral vegetation. Precipitation was near 70 cm annually as compared with 33 cm in the area today and mean annual temperature was fully 5.5°C lower than at present (Axelrod 1976: fig. 5). A flora of comparable age is represented in the Santa Cruz Mountains near Saratoga (Dorf 1930). It records forest taxa (*Libocedrus, Pinus* cf. *lambertiana, Pseudotsuga*) at much lower altitudes than occur near sea level in this area today. By contrast, the fossil site supports oak woodland–

grass and broadleaved sclerophyll forest. Redwood forest is now at higher levels, and is not represented in the fossil flora.

The magnitude of the climatic shift along the coastal strip in the Early Pleistocene is indicated by a flora from the marine upper Pico Formation (Early Pleistocene, 1 m. y.), situated near Seacliff on the coast west of Ventura (Axelrod 1983). Several cones of Douglas fir (*Pseudotsuga menziesii*) are represented, a species that now has scattered populations in the Santa Lucia Mountains 325 km north but has its principal southern area in the Santa Cruz Mountains 450 km north. Associates in the coastal strip were three pines that are of coastal occurrence today, Monterey pine (*Pinus radiata*), Island pine (*P. remorata*), and Stanton pine (*Pinus muricata* var. *stantonii*). The Seacliff assemblage suggests that temperature along the coastal strip was approximately 13.5°C as compared with 15°C today and that rainfall totalled 76 cm in contrast to 38 cm at present.

Development of Modern Forest Geography

The conifer forests in the mountains of southern California and Baja California Norte are now perched as discontinuous stands on isolated mountain ranges at altitudes generally above 1500 m. At lower altitudes, semidesert, chaparral and woodland vegetation thrive under warmer, drier climates. The discontinuous montane forests have similar dominants, notably *Abies concolor, Calocedrus decurrens, Pinus jeffreyi, P. ponderosa, P. lambertiana, P. murrayana, Populus hastata* ("*trichocarpa*") and *P. tremuloides* (see Griffin and Critchfield 1972, Munz 1935, Nelson 1922, Wiggins 1980). In addition, many forbs, herbaceous perennials, and shrubs link these montane forests.

The now-isolated forest taxa once had a more continuous distribution in the Late Pliocene–Early Pleistocene when climate was considerably wetter and cooler than at present, as demonstrated by the Soboba flora from San Jacinto Valley in interior southern California (Axelrod 1967*a*) and by the limited Chula Vista flora.

In the Plio–Pleistocene transition, mountains were still relatively low, probably scarcely half their present altitudes which now reach up to 3000–3400 m. As colder, wetter climates spread southward, conifer forests shifted from the Sierra Nevada southward into the Tehachapi–Mount Pinos–Liebre Mountain region and thence through the San Gabriel–San Bernardino–San Jacinto Mountains and into the Sierra San Pedro Martir in Baja California Norte (see photos in Nelson 1922). As the fault-block mountains were elevated later to their present heights, the forests were stranded as disjunct stands isolated by drier, warmer climates occupied by woodland, chaparral, sage, and semi-desert vegetation. As the forests were restricted to higher altitudes, some taxa disappeared locally, thus accounting for the present disjunct occurrences in the mountains of southern California (see maps in Griffin and Critchfield 1972, Little 1971, also discussion in Munz 1935). Other disjunct distributions of Sierran montane taxa in the mountains of southern California are exemplified by *Acer glabrum, Cornus nuttallii, Euonymus occidentalis, Phyllodoce breweri, Rhododendron occidentale, Prunus emarginata,* and many forbs, herbaceous perennials and shrubs listed by Munz (1935). Greater disjunctions from the southern Sierra Nevada are seen in the distribution of *Pinus murrayana* (San Gabriel, San Bernardino, San Jacinto mountains, and San Pedro Martir) and *Populus tremuloides* (San Bernardino Mountains and San Pedro Martir).

Evolution and Biogeography of *Pinus radiata*

The Chula Vista flora provides additional evidence regarding the probable evolutionary history of the five living populations of *Pinus radiata.* Based on their cones these populations can be separated into two groups. The populations of *P. radiata* on Cedros Island (var. *cedrosensis*) and on Guadalupe Island (var. *binata*) represent one group characterized by small symmetrical to slightly asymmetrical cones without prominent apophyses except for the extreme variation seen in var. *binata.* By contrast, the other group represented by the California populations at Monterey, Año Nuevo and Cambria possess larger, regularly asymmetrical cones with large, rounded apophyses.

Table 3. Trees and shrubs in coastal southern California with close relatives in equable montane areas of Mexico.

California	Mexico
Arbutus menziesii	*A. xalapensis*
Ceanothus arboreus	*C. caeruleus*
Cercocarpus traskiae	*C. mojadensis*
Comarostaphylis diversifolia	*C.* spp. (12 or more)
Myrica californica	*M. mexicana*
Pinus remorata	*P. oocarpa*
Pinus torreyana	*P. oxacana*
Prunus lyonii	*P. prionophylla*
Vaccinium ovatum	*V. confertum*

There is considerable similarity between *Pinus radiata* var. *cedrosensis* and *P. remorata* Mason which has large populations in Pine Canyon west of Lompoc, on Santa Cruz and Santa Rosa islands, and in Baja California near the coast southwest of San Vicente. Cones of Cedros Island pine differ from those of *P. remorata* in having somewhat more prominent apophyses and slightly thicker cone scales. These differences seem to reflect the different environments to which these pines are adapted, with the cooler, foggier, moister climate in the north favoring the persistence of a more "primitive type," as exemplified by *P. remorata.* Cones of *P. remorata* are similar to those of *P. oocarpa,* though in its northern areas *P. oocarpa* cones approach those of *P. radiata* var. *cedrosensis* in having more prominent apophyses (see U.C. Herbarium) than in areas to the south.

The geologic ages of these pines are not presently known, but to judge from their relation to *Pinus oocarpa* and their present disjunct distribution (see Martinez 1948), they have probably been in existence since the Middle Miocene. Up to 500 km of right-lateral strike-slip movement since the Middle Miocene along the San Andreas fault system and related rifting in the Gulf of California is probably in large part responsible for the present biogeography (Gastil and Jensky 1973). The fact that Baja California was once part of the Mexican mainland is supported by floristic evidence that provides additional data with respect to derivation of Monterey pines from ancient members of *Pinus* subsect. Oocarpeae. Geologic evidence indicates that a chain of low coastal mountains was once situated west of the San Andreas rift. These hills were probably covered with taxa that now have closely allied species in southern California and in the mountains of Mexico, chiefly in areas of equable climate (Table 3).

Today, these allied taxa are now isolated by the broad stretch of the Sonoran Desert and adjacent Thorn Forest vegetation. Links are also provided by a number of taxa now in Mexico that have allied fossil species in the Miocene Puente and Modelo floras of coastal southern California (Axelrod 1977:162), distributed in *Clethra, Magnolia, Nectandra, Persea, Quercus, Sabal* and others. They clearly indicate that a humid, equable Miocene route connected these areas. That there was a near-coastal route is indicated also by the Mint Canyon (Axelrod 1979:25, 32) and Tehachapi floras (Axelrod 1939). They demonstrate that by 19 m.y. ago—and certainly earlier—interior southern California–Arizona was too semiarid and hot for the taxa noted above. Hence, allies of the mesic species now in coastal California or in Mexico shifted into coastal southern California via a near-coastal, not an interior route. It was this route that brought pines of subsect. Oocarpeae to California.

At that time, it is inferred that the ancestor of *Pinus radiata* var. *cedrosensis* was in the mountains, living under a mild, warm temperate climate. Insularity developed from opening of the Gulf of California (since 5 m.y.), and submergence of the outer continental shelf. There the pine has persisted on the higher summits of Cedros Island where it is sheltered by a regular summer fog belt at altitudes above 600 m. The smaller cones of the Cedros and Guadalupe Island pines seemingly reflect their closer relation to *P. oocarpa* which was not far away in the mountains of Sonora–Sinaloa, to which

Baja California was joined in the Miocene. Further, their small size may reflect the summer rain regime to which they are and were adapted.

Pinus diegensis, closely allied to *P. radiata* var. *binata,* may have been derived from var. *cedrosensis* by adaptation to somewhat greater aridity over the northern part of the earlier distribution of the immediate ancestor of var. *cedrosensis.* This may account for the greater variation in symmetry and apophyses development in *P. radiata* var. *binata.* That *P. diegensis* (cf. *binata*) may represent the ancestral form that gave rise to the three California populations of *Pinus radiata* is suggested by its Pliocene mainland occurrence, and by its cone variation which is intermediate between var. *cedrosensis* and the type Monterey population.

Cones of the three California populations of *Pinus radiata,* which are larger, more asymmetrical, and have prominent apophyses, presumably reflect adaptation to a progressively more extreme mediterranean climate of dry summers. In the suggested evolutionary sequence—*oocarpa–remorata–cedrosensis–binata–Monterey–Año Nuevo–Cambria*—it is noteworthy that *Pinus diegensis* approaches the variation of the Monterey population. This lends further, though still tenuous, support to its probable place in the evolution of Monterey pines.

The fossil samples now available suggest that *Pinus radiata* populations with cones comparable in size, symmetry, and apophyses development to the Guadalupe and Monterey populations were rather widespread in coastal California well into the Pleistocene. At Carpinteria cones more nearly approaching the larger-sized Año Nuevo population appear only late in the Pleistocene (Axelrod 1980*a*). Cones the size of the present Cambria population are not now known as fossils. They may be the most recent of the group, possibly originating in post-glacial time.

Conclusion

In the Late Pliocene (ca. 3 m.y.), increased precipitation and lower temperatures in California enabled floras of more mesic, cooler requirements to replace floras adapted to drier, warmer climate, as illustrated by the Mulholland (Axelrod 1944*a*), Oakdale (Axelrod 1944*b*), Piru Gorge (Axelrod 1950*d*) and Mount Eden (Axelrod 1937, 1950*b*) floras. The more mesic, younger floras, like the Santa Rosa, Napa, Upper Wildcat, Turlock and (probably) Coalinga, still have a few exotic taxa allied to species in summer rain areas, reflecting a warmer sea surface than that of today. Owing to its more southerly position, the influence of cooler climate at Chula Vista was not so pronounced, though precipitation was about double that of today. The lowland flora of southern California then represented a different floristic province than that to the north, one adapted to a warmer climate, much as comparable thermal differences separate the floras of northern and southern California today.

The succeeding colder, wetter climate of the latest Pliocene and early Pleistocene enabled Douglas fir (*Pseudotsuga menziesii*) forest to shift south into coastal southern California, fully 350 km (or somewhat more) south of its present scattered coastal stations. Over the interior, lowered temperature and higher precipitation enabled the Sierran mixed conifer forest to range southward into the mountains of southern California and Baja California Norte. The Sierran mixed conifer forest then lived fully 1000 m below its present level at a time when mountains were appreciably lower. The present forests were stranded as isolated patches as the discontinuous mountains were uplifted in the middle and later Quaternary and drier, hotter climates spread over the region. These later, more extreme conditions probably account for the present disjunct occurrences of diverse montane taxa in the mountains of southern and Baja California, and for the restriction of taxa allied to those in the Chula Vista flora to more local areas.

Evidence suggests that *Pinus diegensis* (cf. *P. radiata* var. *binata*) may have given rise to the California populations of *Pinus radiata* by progressive adaptation to increasing summer drought. Further, *P. radiata* var. *binata* did not originate in insular

isolation, but like many other insular endemic trees and shrubs, was confined there by unfavorable land climates during the past.

Systematics

Family Pinaceae

Pinus diegensis new species
Figures 6A, B, 7A, B

Description.—Cones long-oval to elliptic oval; small cone (SDSNH 25135) 9 cm long and 5 cm broad, medium sized cone (SDSNH 25165) about 10–11 cm long (estim.), and about 6.5 cm broad; largest cones (SDSNH 25136, 25137) somewhat flattened, fragmentary. Cone scales up to 4.0–4.5 cm long and 2.0–2.3 cm broad, distally. Tips of cone scales broadly flattened, with slightly swollen, convexly rounded apophyses well inside tip of scale.

Types.—Holotype SDSNH no. 25135, Paratypes SDSNH no. 25110, 25136, 25137, 25165.

Discussion.—Four incomplete cones are sufficiently distinct from those previously described to warrant the recognition of a new species. Examination of the large, excellent collection of pine cones in the herbarium of the U.S. Forest Service, Institute of Genetics, Placerville, California, indicates that *P. diegensis* is a member of the subsect. Oocarpeae (Little and Critchfield 1969). The fossil cones are most similar to the variable cones produced by *Pinus radiata* var. *binata* Engelmann from Guadalupe Island. The variation present in the small fossil collection is readily duplicated by the large suites of cones that have been recovered from the island.

Howell (1941*a*) discussed cone variation in the Guadalupe pine, noting that asymmetrical cones with large apophyses on the outer side (like fig. 6B) were similar to the type which comes from Monterey. A second form with nearly symmetrical cones (like fig. 6A) and with scales alike on all sides and with little prominent apophyses development Howell termed *forma guadalupensis.* A third form, intermediate between the latter two he termed *forma binata,* noting that it corresponded with the type specimen collected from Guadalupe. As discussed separately in the section on Evolution, the variable *binata* on Guadalupe Island may represent a population close to that which gave rise to the three living populations in central California.

In southern California, fossil pine cones allied to the present California populations of *Pinus radiata* have been recorded previously from the late Tertiary Mount Eden (Axelrod 1937) and Lower Pico floras (Dorf 1930). It is also known from Pleistocene floras at Carpinteria (Chaney and Mason 1933), near Seacliff on the coast west of Ventura (Axelrod 1983), and at Rancho La Brea (Mason 1927). In coast-central California, it is known from Mussel Rock on the outer coast south of San Francisco. Here it has been recovered from an old forest soil that rests on Franciscan diabase and is overlain by the basal beds of the marine Merced Formation, approximately 5–6 m.y. old (Axelrod 1967*b*). Pleistocene records in central California are near Pt. Sal (Axelrod 1967*b*), Little Sur (Langenheim and Durham 1963), Millerton (Mason 1934, Axelrod 1980*a*), and Drakes Bay (Axelrod 1980*a,* 1983).

The present record is the most southern fossil locality now known for species of Monterey pine.

Pinus jeffreyoides new species
Figures 7C, D

Description.—Cone large, estimated 15–10 cm long and fully 10 cm broad; cone scales large, up to 4 cm long in central part of cone; terminal part of cone scale broadly triangular, 1.5–2.5 cm wide and 0.8–1.1 cm thick as measured below the umbo.

Types.—Holotype SDSNH 25166; Paratypes SDSNH 25138, 25167.

Discussion.—This is a member of subsect. Ponderosae Little and Critchfield (1969) and is well-matched by cones of the living *Pinus jeffreyi* Greville and Balfour. Rela-

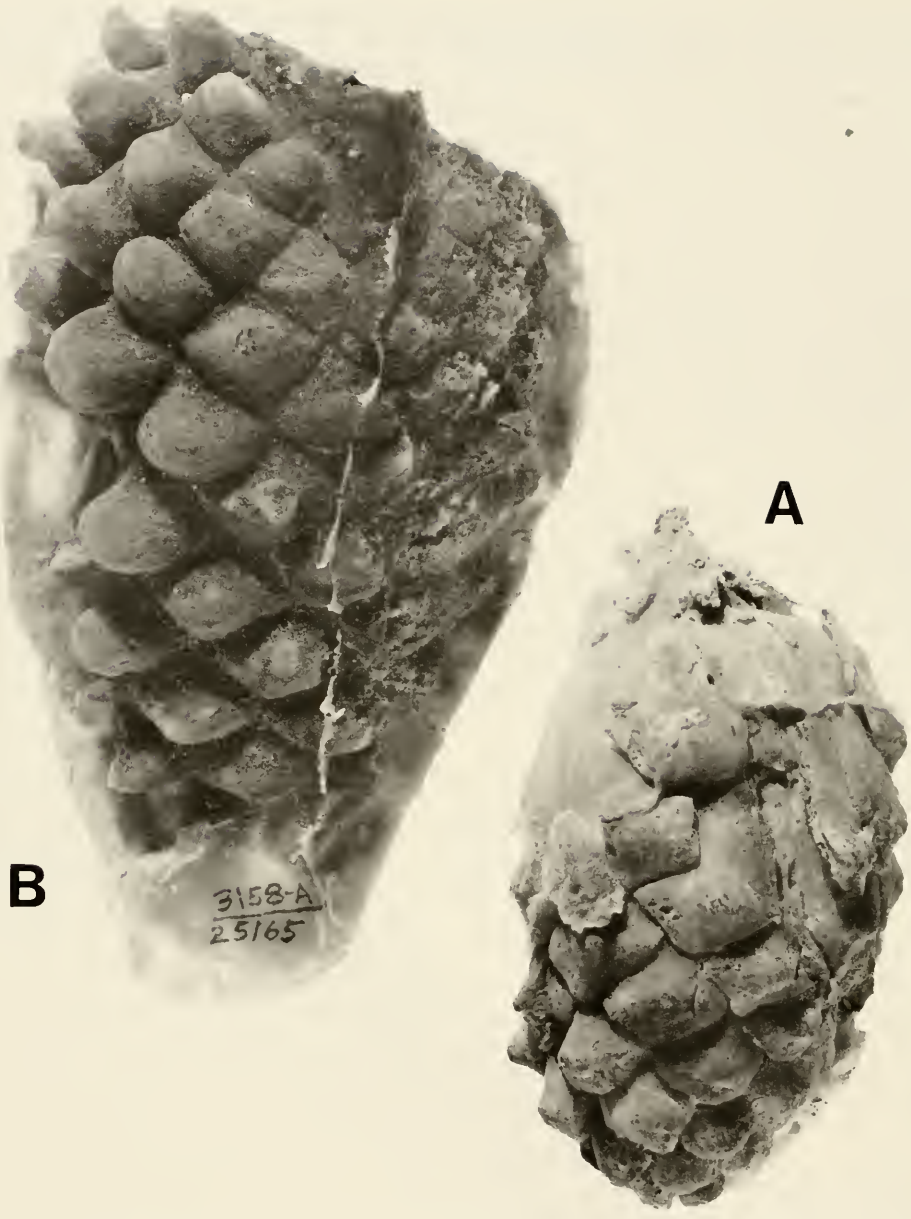

FIGURE 6. A,B—*Pinus diegensis* new species, A—holotype, SDSNH 25135, B—paratype, SDSNH 25165. All specimens ×1 (latex casts).

tionship with *P. jeffreyi* is apparent in the morphology of the distal ends of the cone scales, which are much thicker than those of the allied *P. ponderosa* Lawson.

Pinus pieperi Dorf
Figures 7B

Pinus pieperi Dorf, Carnegie Inst. Wash. Publ. 412, p. 69, pl. 5, figs. 7–10, 1930; Axelrod, Carnegie Inst. Wash. Publ. 476, p. 156, pl. 2, figs. 2, 3, 1937.

Referred specimen.—SDSNH 25168.

Remarks.—A single fragment of a cone with distinctive cone scales that have

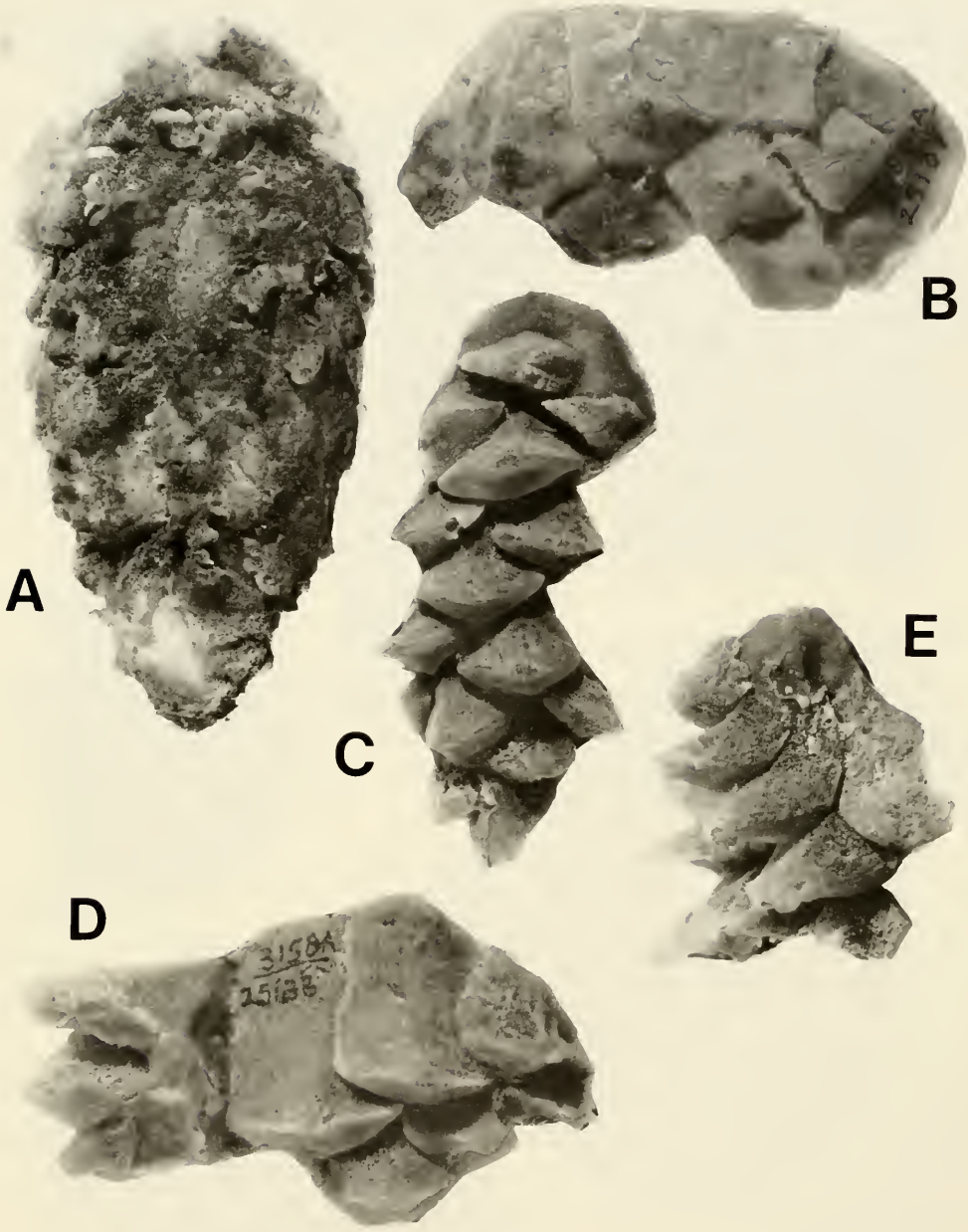

FIGURE 7. A,B—*Pinus diegensis* new species, A—paratype, SDSNH 25110, B—paratype, SDSNH 25137; C,D—*Pinus jeffreyoides* new species, C—holotype, SDSNH 25166, D—paratype, SDSNH 25138; E—*Pinus pieperi* Dorf, SDSNH 25168. All specimens ×1 (latex casts).

prominently hooked, large apophyses represents this species which is allied to digger pine, *Pinus sabiniana* Douglas of central California. The specimen measures 6.0 cm long and 5.5 cm wide.

Pinus pieperi has been recorded previously in southern California from the Plio–Pleistocene rocks north of Ventura (Wiggins 1951), in the lower part of the Pico Formation west of Ventura (Dorf 1930), in the upper Pico Formation near Seacliff on the coast west of Ventura (Axelrod 1983), as well as in the Mount Eden flora near Beaumont (Axelrod 1937). A fragmentary cone scale from the Anaverde Formation near Palmdale

has also been referred to *Pinus pieperi* (Axelrod 1950*c*). Digger pine may have been eliminated from southern California as drier hotter climate spread there during the Xerothermic.

Family Arecaceae
Gen. et sp. indet.
Figure 8A

Referred specimen.—SDSNH 25163.

Remarks.—A fragmentary specimen that certainly represents a palm is in the collection. It is 7 cm long and 2.5 cm broad, the blade has 4 rays each with a prominent midvein and each is bordered by 7–8 fine parallel veins that are somewhat less than 1 mm apart.

Comparison with several genera indicates that it may represent a species of *Sabal* or *Brahea* (=*Erythea*), but in view of the incomplete nature of the fossil reference to either (or any) genus seems unjustified. Both of the noted genera extend up into oak woodland vegetation, *Sabal* in northern Sinaloa and adjacent Sonora, *Brahea* in the highlands of southernmost Baja California, and both regions with ample rainfall in summer. In addition, *Brahea* is associated with Monterey pine on Guadalupe Island.

Family Juncaceae
Gen. et. sp. indet.
Figure 8B

Referred specimen.—SDSNH 25164.

Remarks.—A single slender reed-like leaf impression is 5 cm long and 7 mm wide with 9–10 parallel veins. The blade is without a midrib and clearly represents a sedge- or reed-like plant of indeterminate nature. It seems comparable to some leaves of *Cyperus,* and especially to *Juncus,* both common in marshy areas and on banks along slow, meandering rivers.

Family Salicaceae
Populus alexanderi Dorf
Figures 8E, F

Populus alexanderi Dorf, Carnegie Inst. Wash. Publ. 412, p. 75, pl. 6, fig. 11 only, 1930; Axelrod, Carnegie Inst. Wash. Publ. 553, p. 281, pl. 48, fig. 4, 1944; Axelrod, Univ. Calif. Publ. Geol. Sci. 34, p. 128, pl. 19, figs. 1–11, 1958.

Referred specimens.—SDSNH 25159, 25160, 25161, 25162.

Remarks.—This fossil species represents a cottonwood similar to the coastal *Populus trichocarpa* Torrey and Gray, the type of which comes from the Santa Clara River near Ventura. This species differs from leaves commonly identified as *P. alexanderi* and *P. eotremuloides* Knowlton in its ovate shape and smaller size as compared with the lanceolate-ovate form of the species from Miocene floras to the north and in the north coast Pliocene floras as well. The specimens from the Verdi flora (Axelrod 1958, pl. 19) illustrate the nature of the species, and the accompanying plate 20 (loc. cit.) shows how much *Populus* "*trichocarpa*" from the mountains differs from it; this montane and north coastal species seems to represent *P. hastata* Dode.

P. alexanderi (restricted) is indicative of a climate with mild winters as compared with *P. eotremuloides* which inhabited areas with colder climate. The ovate-leaved *P. alexanderi* is related to *P. emersoni* Condit from the San Pablo flora (Condit 1938; Lesquereux 1883, pl. 55, figs. 3, 5, only), though the latter has consistently larger leaves.

Salix wildcatensis Axelrod
Figures 8C, D

Salix wildcatensis Axelrod, Carnegie Inst. Wash. Publ. 553, p. 132, 1944 (see synonymy); Chaney, Carnegie Inst. Wash. Publ. 553, p. 341, pl. 58, Fig. 2, 1944.

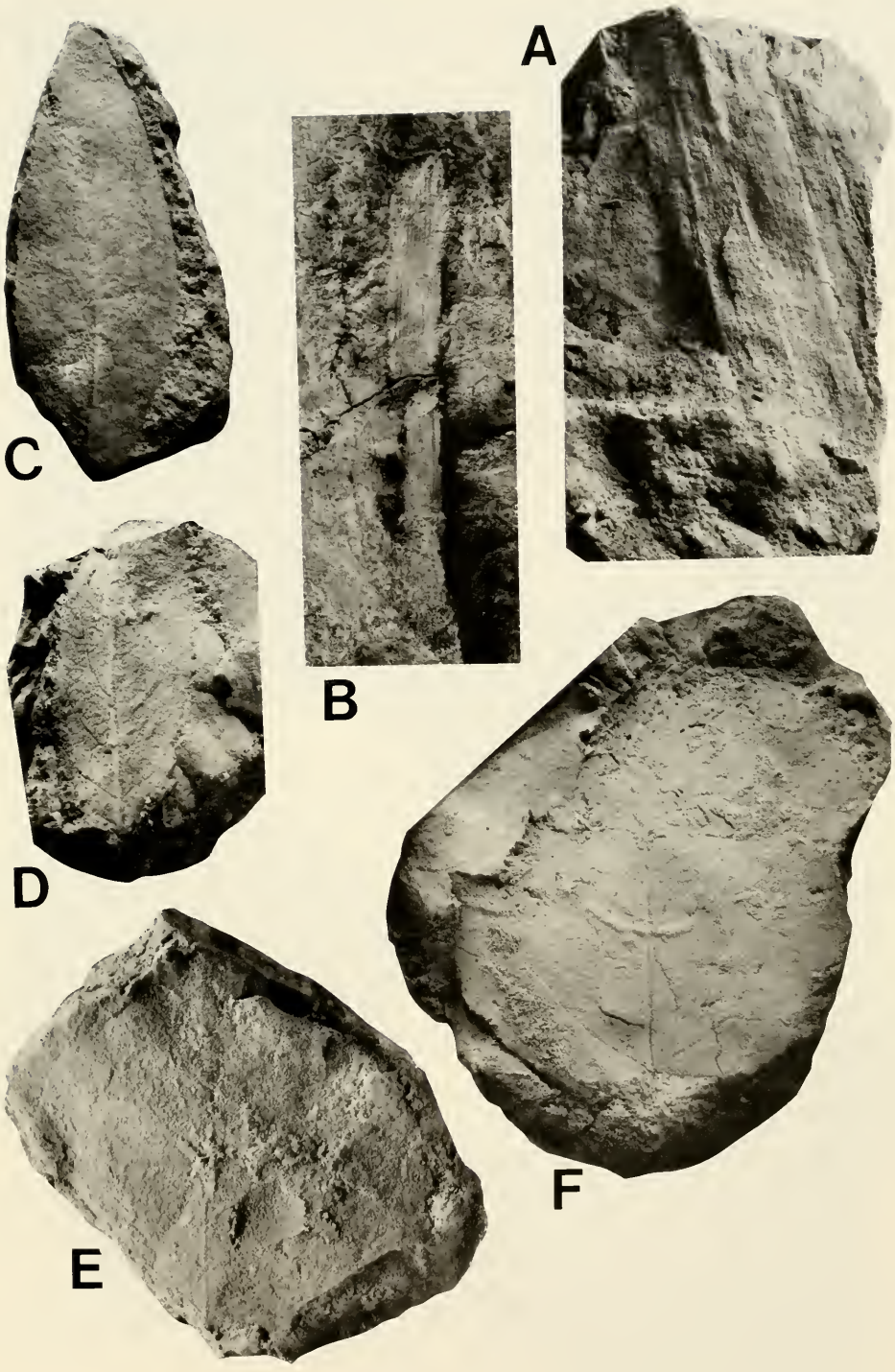

FIGURE 8. A—Arecaceae indet., SDSNH 25163; B—Juncaceae indet., SDSNH 25164; C,D—*Salix wildcatensis* Axelrod, C—SDSNH 25153, D—SDSNH 25152; E,F—*Populus alexanderi* Dorf, E—SDSNH 25159, F—SDSNH 25160. All specimens ×1.

Salix coalingensis Dorf (in part), Carnegie Inst. Wash. Publ. 476, p. 170, pl. 4, fig. 8, 1937.

Referred specimens.—SDSNH 25152, 25153, 25154.

Remarks.—Three fragmentary specimens, the largest 7.0 cm long and 2.6 cm broad, represent this willow. It is allied to *Salix lasiolepis* Bentham, a common shrub to small tree that is widely distributed in the Coast Ranges and lower Sierra Nevada, reaching southward into the coastal slopes of northern Baja California. It is also disjunct to southeastern Arizona. In both areas it is a common member of riparian vegetation in oak woodlands.

Family Fagaceae
Quercus lakevillensis Dorf
Figure 9C

Quercus lakevillensis Dorf, Carnegie Inst. Wash. Publ. 412, p. 82, pl. 8, figs. 4, 5, 1930; Axelrod, Carnegie Inst. Wash. Publ. 590, p. 58, pl. 3, fig. 4, 1950; Axelrod, Univ. Calif. Publ. Geol. Sci. 121, p. 165, pl. 18, figs. 2, 3, 1980.

Referred specimen.—SDSNH 25158.

Remarks.—A single leaf in the flora is similar to those produced by the common California live oak, *Quercus agrifolia* Neé. The specimen is oval in outline, has broad sinuses and wavering, irregular secondaries that diverge at moderate angles. The modern species is common in the Coast Ranges from Sonoma County southward into Baja California. Near the coast, where it is subject to regular summer fog, it forms pure dense woodlands. Elsewhere it is a member of diverse communities, including redwood forest, closed cone pine forest, broadleaved sclerophyll woodland and occurs also in the coastal sectors of digger pine woodland.

Family Lauraceae
Persea coalingensis (Dorf) Axelrod
Figures 9A, B

Persea coalingensis (Dorf) Axelrod, Carnegie Inst. Wash. Publ. 553, p. 132, 1944 (see synonymy and discussion); Axelrod, Univ. Calif. Publ. 121, p. 112, pl. 12, fig. 4; p. 167, pl. 19, fig. 7; pl. 20, figs. 2–4, 1980.

Referred specimens.—SDSNH 25149, 25150, 25151.

Remarks.—The long-elliptic leaves of avocado are the commonest leaf fossil in the Chula Vista flora. Most were broken during transport into the marine basin though sufficient details of venation are present to permit their certain reference to this late Tertiary species. Two nearly complete specimens tentatively grouped under *Persea* may represent *Magnolia* but the finer details of venation which would make their identification certain are not preserved.

Family Platanaceae
Platanus paucidentata Dorf
Figures 10D, E

Platanus paucidentata Dorf, Carnegie Inst. Wash. Publ. 412, p. 94, pl. 10, figs. 4, 9; pl. 11, fig. 1; pl. 12, fig. 1, 1930; Axelrod, Carnegie Inst. Wash. Publ. 476, p. 174, pl. 5, figs. 4, 5, 1937; Axelrod, Univ. Calif. Publ. Geol. Sci. 121, p. 113, pl. 13, fig. 1; p. 168, pl. 20, fig. 1, pl. 21, fig. 7, 1980.

Referred specimens.—SDSNH 25155, 25156, 25157.

Remarks.—The typical lobed leaves of this sycamore are in the flora. The large leaves regularly produced by the species were broken and mangled during transport into the marine basin. However, the distinctive primary venation and the lobed nature of the leaves permits their ready identification.

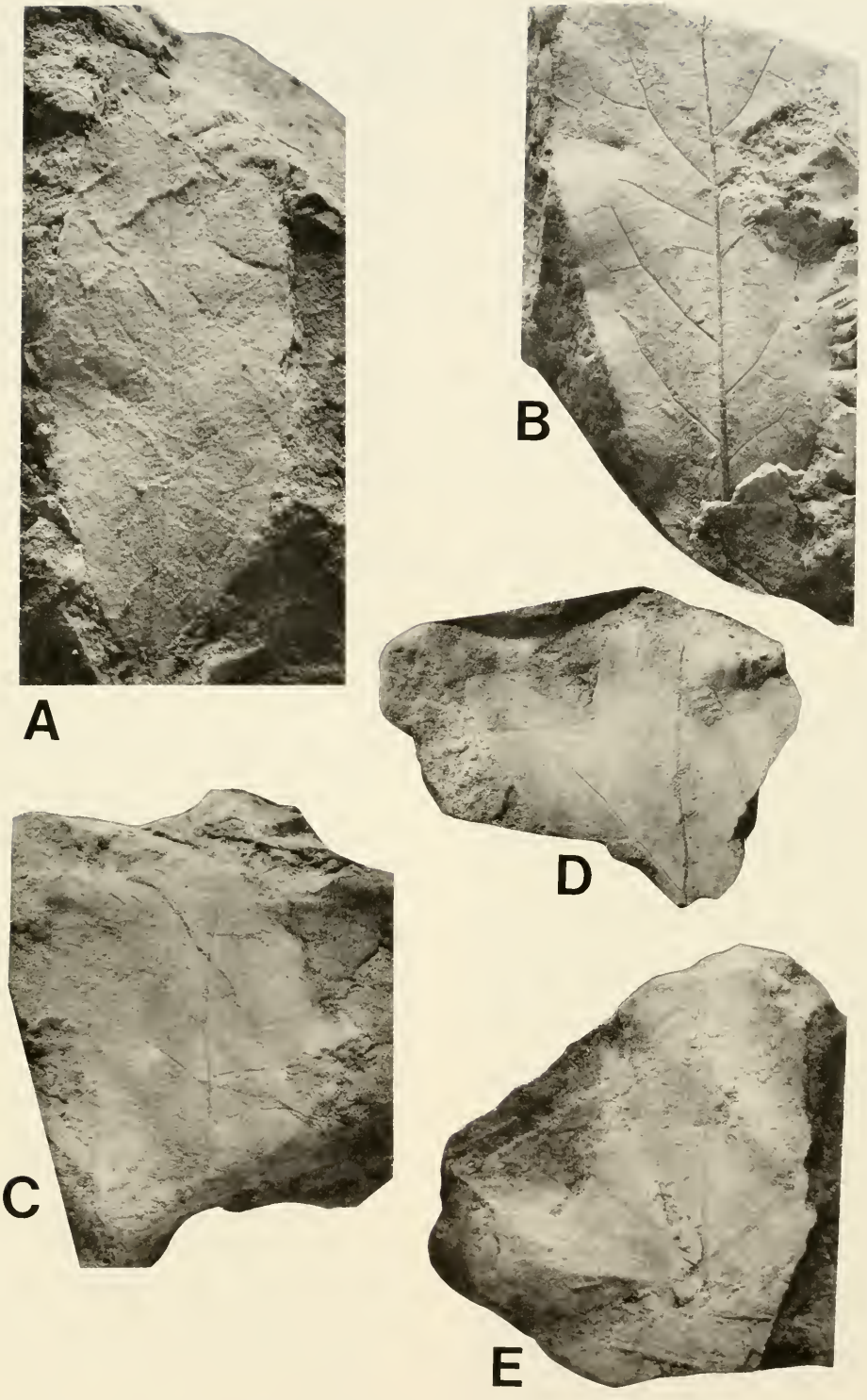

FIGURE 9. A,B—*Persea coalingensis* (Dorf) Axelrod, A—SDSNH 25150, B—SDSNH 25151; C—*Quercus lakevillensis* Dorf SDSNH 25158; D,E—*Platanus paucidentata* Dorf, D—SDSNH 25155, E—SDSNH 25157. All specimens ×1.

The fossil species has leaves similar to those of *Platanus racemosa* Nuttall, found along stream banks and floodplains in oak woodland vegetation from central California southward into Baja California. An allied species. *P. wrightii* Watson, is in Arizona and border areas. The fossil species, *P. paucidentata,* is common in the Miocene and Pliocene floras of California.

Acknowledgments

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Literature Cited

Axelrod, D. I. 1937. A Pliocene flora from the Mount Eden beds, southern California. Carnegie Institution of Washington Publication 476:125–183.

———. 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Institution of Washington Publication 516:129.

———. 1944*a*. The Mulholland flora. Carnegie Institution of Washington Publication 553:103–145.

———. 1944*b*. The Oakdale flora. Carnegie Institute of Washington Publication 553:147–165.

———. 1944*c*. The Sonoma flora. Carnegie Institute of Washington Publication 553:167–206.

———. 1950*a*. A Sonoma florule from Napa, California. Carnegie Institute of Washington Publication 590:23–71.

———. 1950*b*. Further studies of the Mount Eden flora, southern California. Carnegie Institute of Washington Publication 590b:73–117.

———. 1950*c*. The Anaverde flora of southern California. Carnegie Institute of Washington Publication 590:119–158.

———. 1950*d*. The Piru Gorge Flora of southern California. Carnegie Institute of Washington Publication 590:159–214.

———. 1958. The Pliocene Verdi flora of western Nevada. University of California Publications in Geological Sciences 34:91–160.

———. 1967*a*. The Pleistocene Soboba flora of southern California. University of California Publications in Geological Sciences 60:1–108.

———. 1967*b*. Evolution of the Californian closed-cone pine forest. Pp. 93–150 *in* R. N. Philbrick, (ed.). Proceedings of the Symposium on Biology of the California Islands. Santa Barbara Botanical Garden.

———. 1976. History of the coniferous forest, California and Nevada. University of California Publications in Geological Science 70:1–62.

———. 1977. Outline history of California vegetation. Pp. 139–193 *in* M. G. Barbour and J. Major (eds.). Terrestrial Vegetation of California. J. Wiley & Sons, New York.

———. 1979. Age and Origin of Sonoran Desert Vegetation. California Academy of Sciences Occasional Papers 132:1–74.

———. 1980*a*. History of the maritime closed-cone pines, Alta and Baja California. University of California Publications in Geological Sciences 120:1–143.

———. 1980*b*. Contributions to the Neogene Paleobotany of Central California. University of California Publications in Geological Sciences 121:1–212.

———. 1983. New Pleistocene conifer records, coastal California. University of California Publications in Geological Sciences 127:1–107.

Bailey, H. P. 1960. A method of determining the warmth and temperateness of climate. Geografiska Annaler 42:1–16.

———. 1964. Toward a unified concept of the temperate climate. Geographical Review 54: 516–545.

Barnes, L. G. 1973. Pliocene cetaceans of the San Diego Formation. Pp. 37–43 *in* Arnold Ross and R. J. Dowlen (eds.). Studies on the geology and geological hazards of the greater San Diego area, California. San Diego Association of Geologists.

———. 1976. Outline of the eastern North Pacific fossil cetacean assemblages. Systematic Zoology 25(4):321–343.

Chaney, R. W., and H. L. Mason. 1933. A Pleistocene flora from the asphalt deposits at Car-

pinteria, California. Carnegie Institute of Washington Publication 415:45–79.

Condit, C. 1938. The San Pablo Flora of West Central California. Carnegie Institute of Washington Publication 476:217–268.

Deméré, T. A. 1983. The Neogene San Diego Basin: A review of the marine Pliocene San Diego Formation. Pp. 187–195 *in* D. K. Larue and R. J. Steel (eds.). Cenozoic marine sedimentation Pacific Margin, U.S.A. Society of Economic Paleontologists and Mineralogists, Pacific Section.

Dorf, E. 1930. Pliocene floras of California. Carnegie Institute of Washington Publication 412: 1–112.

Gastil, R. G., and W. Jensky. 1973. Evidence of strike-slip displacement beneath the trans-Mexican volcanic belt. Stanford University Publications in Geological Sciences 12:171–180.

Gentry, H. S. 1942. Rio Mayo Plants: A study of the flora and vegetation of the Valley of the Rio Mayo, Sonora. Carnegie Institute of Washington Publication 527:1–328.

———. 1946. Notes on the vegetation of Sierra Surotato in northern Sinaloa. Torrey Botantical Club Bulletin 73:451–462.

Grant, U. S., IV, and H. R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. San Diego Society Natural History Memoir 1:1–1036.

Griffin, J. R., and W. B. Critchfield. 1972. The distribution of forest trees in California. USDA, Forest Service Research Paper PSW-82/1972. 118 pp.

Hertlein, L. G., and U. S. Grant, IV. 1944. The geology and paleontology of the marine Pliocene of San Diego, California, Pt. 1, Geology. San Diego Society Natural History Memoir 2: 1–72.

———. 1954. Geology of the Oceanside–San Diego coastal area, southern California. Pp. 53–63 *in* R. H. Jahns (ed.). Geology of Southern California, Chap. II, Geology of the Natural Provinces. California Division of Mines Bulletin 170.

———. 1960. The geology and paleontology of the marine Pliocene of San Diego, California, Pt. 2a, Paleontology. San Diego Society Natural History Memoir 2a:73–133.

———. 1972. The geology and paleontology of the marine Pliocene of San Diego, California, Pt. 2b, Paleontology. San Diego Society Natural History Memoir 2b:143–409.

Howard, H. 1949. New avian records for the Pliocene of California. Carnegie Institute of Washington Publication 584:177–199.

Howell, J. T. 1941*a*. The closed-cone pines of insular California. Leaflets of Western Botany 3:1–8.

———. 1941*b*. My visits to Guadalupe Island. Leaflets of Western Botany 3:36–41.

Ingle, J. C., Jr. 1967. Foraminiferal biofacies, variations and the Miocene–Pliocene boundary in southern California. Bulletin American Paleontology 52(236):216–394.

Keen, A. M., and H. Bentson. 1944. Checklist of California Tertiary marine Mollusca. Geological Society of America Special Papers 56:1–280.

Kennedy, M. P. 1975. Geology of the San Diego Metropolitan area, California, Section A. California Division Mines and Geology Bulletin 200:9–39.

Lajoie, K. R., A. M. Sarna-Wojcicki, and R. F. Yerkes. 1982. Quaternary chronology and rates of crustal deformation in the Ventura area, California. Neotectonics of the Ventura Basin. Field Trip No. 3:43–51. Guidebook for 78th Ann. Meeting Cordilleran Section, Geological Society of America, Anaheim, California.

Langenheim, J. H., and J. W. Durham. 1963. Quaternary closed-cone pine forest from travertine near Little Sur, California. Madrono 17: 33–51.

Lesquereux, L. 1883. Contributions to the fossil flora of the Western Territories. III. The Cretaceous and Tertiary floras. U.S. Geological Survey of Territories, vol. 8:1–283.

Libby, W. J., M. H. Bannister, and Y. B. Linhart. 1968. The pines of Cedros and Guadalupe Islands. Journal of Forestry 66:846–853.

Little, E. L., Jr. 1971. Atlas of United States Trees. U.S. Department of Agriculture Forest Service, Miscellaneous Publication 1146. 200 maps.

———, Jr., and W. B. Critchfield. 1969. Subdivisions of the genus *Pinus* (Pines). U.S. Department of Agriculture Forest Service, Miscellaneous Publication 1144:1–51.

Mandel, D. J., Jr. 1973. Latest Pliocene Foraminifera in the upper part of the San Diego Formation, California. Pp. 33–36 *in* A. Ross and R. J. Dowlen (eds.). Studies on the geology and geologic hazards of the greater San Diego area, California. San Diego Association of Geologists.

Martinez, M. 1948. Los Pinos Mexicanos. 2nd ed. Mexico: Ediciones Botas. 316 pp.

Mason, H. L. 1927. Fossil records of some west American conifers. Carnegie Institute of Washington Publication 346:139–158.

———. 1934. Pleistocene flora of the Tomales Formation. Carnegie Institute of Washington Publication 415:81–179.

Miller, L. 1956. A collection of bird remains from the Pliocene of San Diego, California. California Academy of Sciences Proceedings 28(16): 615–621.

Munz, P. A. 1935. A Manual of Southern California Botany. Claremont, California, Claremont College.

Nelson, E. W. 1922. Lower California and its Natural Resources. National Academy of Sciences Memoir 16:1–194.

U.S. Department of Agriculture, Weather Bureau. 1938. Atlas of Climatic Charts of the Oceans. W.B. No. 1247. 130 charts.

U.S. Navy. 1956–58. Climatic Atlas of the World. Washington, D.C.

Vedder, J. G. 1972. Review of stratigraphic names and megafaunal correlation of Pliocene rocks along the southeast margin of the Los Angeles basin, California. Pp. 158–172, *in* E. H. Stinemeyer (ed.). Pacific Coast Miocene Biostrati-

graphic Symposium. Society of Economic Paleontologists and Mineralogists.

Wiggins, I. L. 1951. An additional specimen of *Pinus pieperi* Dorf from Ventura County, California. American Journal of Botany 38:211–213.

———. 1980. Flora of Baja California. Stanford: Standford Univ. Press. 1025 pp.

Woodring, W. P., and M. N. Bramlette. 1951. Geology and paleontology of the Santa Maria district, California. U.S. Geological Survey Professional Paper 222:1–185.

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Relationships within Eumalacostracan Crustacea

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Abstract. A cladistic analysis was performed on 20 constituent higher taxa within the Eumalacostraca based on 31 characters of external anatomy. Variants of the most parsimonious scheme are presented, and the effects of tolerating different levels of uncertainty are evaluated. It is concluded that: 1) while the basic outline of Calman's (1904) taxonomy of Eumalacostraca might be utilized, the arrangement within peracarids postulated by Siewing (1956) cannot be maintained; 2) the *Baupläne* approach of Schram (1981) has some merit and some of the controversial higher taxonomic groupings of eumalacostracan "orders" originally indicated by that method are vindicated; 3) the idea that the carapace is a derived feature within eumalacostracans, advanced by Dahl (1983), can be maintained only if a high level of homoplasy is tolerated; 4) the concept of a taxon Mysidacea seems best abandoned.

Introduction

The basic modern classification of eumalacostracan crustaceans was outlined by Calman (1904, 1909) with little reference at that time to what the details of phyletic relationships between and within groups might have been. However, it was Siewing (1951, 1956) who presented a phylogenetic tree for eumalacostracans widely subscribed to by subsequent authorities (e.g., Fryer 1964, Hessler 1969).

Recently, however, the Calman/Siewing scheme for Eumalacostraca *sensu stricto* has been questioned. Schram (1981) recognized basic structural plans within the Eumalacostraca, but the methodology he employed was limited by the number of characters that could be handled essentially by pencil and paper. However, the method was helpful in three respects. First, it illustrated a variable range of possible dendrograms. Each variant dendrogram was constrained by which characters received initial emphasis and, thus, demonstrated the basic range of uncertainty that must be implicit in any phylogenetic analysis. Second, the analysis suggested certain "supraordinal" relationships which were a bit unexpected, especially within the peracarid groups. For example, isopods and amphipods were united; and cumaceans, tanaids, and spelaeogriphaceans were allied to each other with some suggestion of more distant possible links of these to thermosbaenaceans. Third, the method also produced a number of "paper" *Baupläne* which were not occupied or had yet to be discovered. Implicit in these hypothetical morphotypes was the idea that if the method had any merit at all, some of those "empty" *Baupläne* might eventually be found.

Watling (1981, 1983) questioned the unity of the superorder Peracarida as a natural taxon. He produced two different cladograms for the peracarids. His stated purpose (in Schram, 1983:347) was to search for ". . . *Baupläne* that include the fine structure . . . ," and he believed that ". . . the first step in the analysis is to look at all these structures for pattern . . . ." In this respect Watling (1983) performed a useful function by focusing attention on characters that had largely been overlooked by previous workers such as mandible function, maxillipede form, and patterns of arterial circulation.

Dahl (1983) formally proposed a concept that had been implicit in several of his earlier papers, viz., that the lack of a carapace is a primitive feature, that the evolution of the carapace had occurred independently several times, and that Calman's caridoid

facies was a set of convergent phenomena. Dahl presented some interesting observations on comparative carapace development related to these ideas. Watling (especially 1983) acknowledged his indebtedness to Dahl's concept of the carapace as a derived feature.

Finally, Hessler (1983) produced a "defense" of the caridoid facies in which he attempted cladistic analysis of the Siewing scheme for peracarids in a more formal manner than had ever been presented before. Hessler's study, however, produced a scheme in which the Siewing arrangement of taxa could be retained only by tolerating a great deal of convergence (10 of his 23 characters are convergent in whole or part to one or more of the others).

Thus, several items bear on the problem of eumalacostracan relationships and demand some sort of a resolution. First, is the need to assess relationships among eumalacostracans by the use of as many characters as possible, and use these characters across-the-board for all taxa, fosssil and Recent. Second, a test is demanded both for Dahl's concept of the carapace as a derived feature, as well as some of the "strange" higher groupings suggested by Schram (1981). And third, it is necessary to arrive at a scheme which will group the taxa in question strictly by their shared derived character states with the fewest number of convergences possible.

Method

One way to analyze large numbers of characters and taxa so as to achieve the most parsimonious arrangement, based solely on shared derived characters, is to use one of the various versions available for the Wagner 78 program. For this analysis, I decided to "break up" certain large and diverse traditional eumalacostracan taxa and treat their components as separate units to test both the viability of such taxa and the "reasonableness" of the characters used. To this end the suborders of Mysidacea (Mysida, Lophogastrida, and Pygocephalomorpha) and of Decapoda as outlined by Burkenroad (1981) (Dendrobranchiata, Eukyphida, Euzygida, and Reptantia) were evaluated as separate entities. The choice of taxa for the decapods was somewhat arbitrary since, for example, Felgenhauer and Abele (1983) break the Eukyphida into two groups coequal with the others, Procarididea and Caridea.

The 31 characters used for this analysis were selected by repeated trial and error (as is standard in any computer-generated cladistic treatment of such data), rejecting potentially useful characters which had low consistency indexes (i.e., high homoplasy values). The ultimate aim of these initial assessments of potentially useful characters was to yield the most parsimonious and congruent cladogram possible. Only characters that could be assessed for all groups relatively unambiguously were used. For example, I did not use the lacinia mobilis because I do not feel its homology has been demonstrated. As has been shown recently (Dahl and Hessler, 1982), this character is not only present in several groups, but is developed differently in these taxa. How can one compare the massive laciniae of lophogastrids with the rather delicate ones in other peracarids? Or, how are larval laciniae to be judged in comparison to those of adults? More needs to be known about the development and functional morphology of laciniae before they can be adequately assessed in a phylogenetic analysis. Other characters were not used because, while they serve to characterize specific taxa, they are quite homoplastic and are known to occur convergently in widely separated groups. For example, the use of the presence of second or third maxillipedes was avoided in the final analysis since it only served to confirm groupings achieved more effectively by singularly derived features. The characters eventually settled upon are given in Table 1, the numbers indicated corresponding to those used in the cladograms.

The program was run using several different outgroups, Hoplocarida, leptostracan Phyllocarida, and a hypothetical ancestor arbitrarily designated primitive for all 31 characters. No differences in any of the resultant eumalacostracan cladograms were noted. Among other parameters, the program also calculated total lengths of trees (i.e., the total number of incidences of derived characters in the cladogram) and the total homoplasy value (i.e., a measure of the total array of convergences and character

TABLE 1. Opposing list of character states used in the analysis of relationships within Eumalacostraca. Numbers correspond to those used in cladograms.

Primitive	Derived
1. Non-caridoid musculature	caridoid musculature
2. No zoeal larvae	zoeae
3. Carapace not fused to all thoracomeres	carapace fused to all thoracomeres
4. No petasma	petasma
5. First thoracomere free of head	first thoracomere fused to head
6. Maxillipede with epipodite	maxillipede without epipodite
7. No brood pouch formed by first pleopod	brood pouch between first pleopod and venter of thorax
8. No scaphognathite	scaphognathite on maxilla
9. First thoracopod unmodified	maxillipedes with lamellate protopod, coxal/basal endites directed mediad
10. Maxillipede endopod robust	maxillipede endopod flagelliform
11. Eggs not brooded on pleopods	eggs brooded on pleopods
12. No caridean lobe	caridean lobe on maxillipede
13. Biramous thoracopods	uniramous thoracopods
14. All pleopods present	pleopods lost or reduced
15. First thoracopod unmodified	maxillipedes with tendency to form gnathobasic endites, endopod pediform
16. Pereiopodal epipodite gills	no pereiopodal epipodite gills
17. First thoracopod unmodified	maxillipedes with basal endites lobate and directed distad
18. No marsupium	oöstegite marsupium
19. Thoracic endopods non-filtratory	thoracic endopods filtratory
20. No male cones	male cones
21. Thoracic coxae unmodified	thoracic coxal plates
22. Eyes stalked or lobed	eyes sessile
23. One pair of uropods	more than one pair of uropods
24. Pleopods non-respiratory	pleopods respiratory
25. Carapace not short	carapace short
26. Eggs not brooded under carapace	eggs brooded under carapace
27. Maxillipedal epipodite if present simple	epipodite specialized as cup- or spoon-like respiratory organ
28. Rostrum simple	pseudorostrum and maxillipedal siphons
29. Thoracic exopods non-respiratory	thoracic exopods respiratory
30. Maxillipedal epipodite as a single segment	epipodite with tendency to form as 2–3 segments
31. Carapace	carapace absent
Character reversal used in analysis portrayed in Figure 3	
31. No carapace	carapace

reversals in the cladogram). These factors proved useful in qualitatively comparing different cladograms.

RESULTS

The computer program generated several variant cladograms. That variant which was most parsimonious and yielded the fewest number of convergences and character reversals is given in Figure 1. In the series of cladograms summarized in Figures 1–3, previous outgroup analysis indicated that the presence of a carapace should be treated as primitive because it is present in all hoplocaridans and phyllocaridans. As can be seen, the program produced (Fig. 1) an unresolved polychotomy with four branches at the base of the Eumalacostraca: eucarids, belotelsonids, syncarids, and waterstonellid/peracarids. A variant of this scheme (Fig. 2) yields an unresolved polychotomy of five branches. Although the latter cladogram has the same number of convergences as the former, it is somewhat shorter than that of Figure 1. A convergence in the secondary reevolution of pereiopodal epipodite gills between Mysida and Amphipoda is traded off for a convergence in the primary loss of pereiopodal epipodite gills in Watersto-

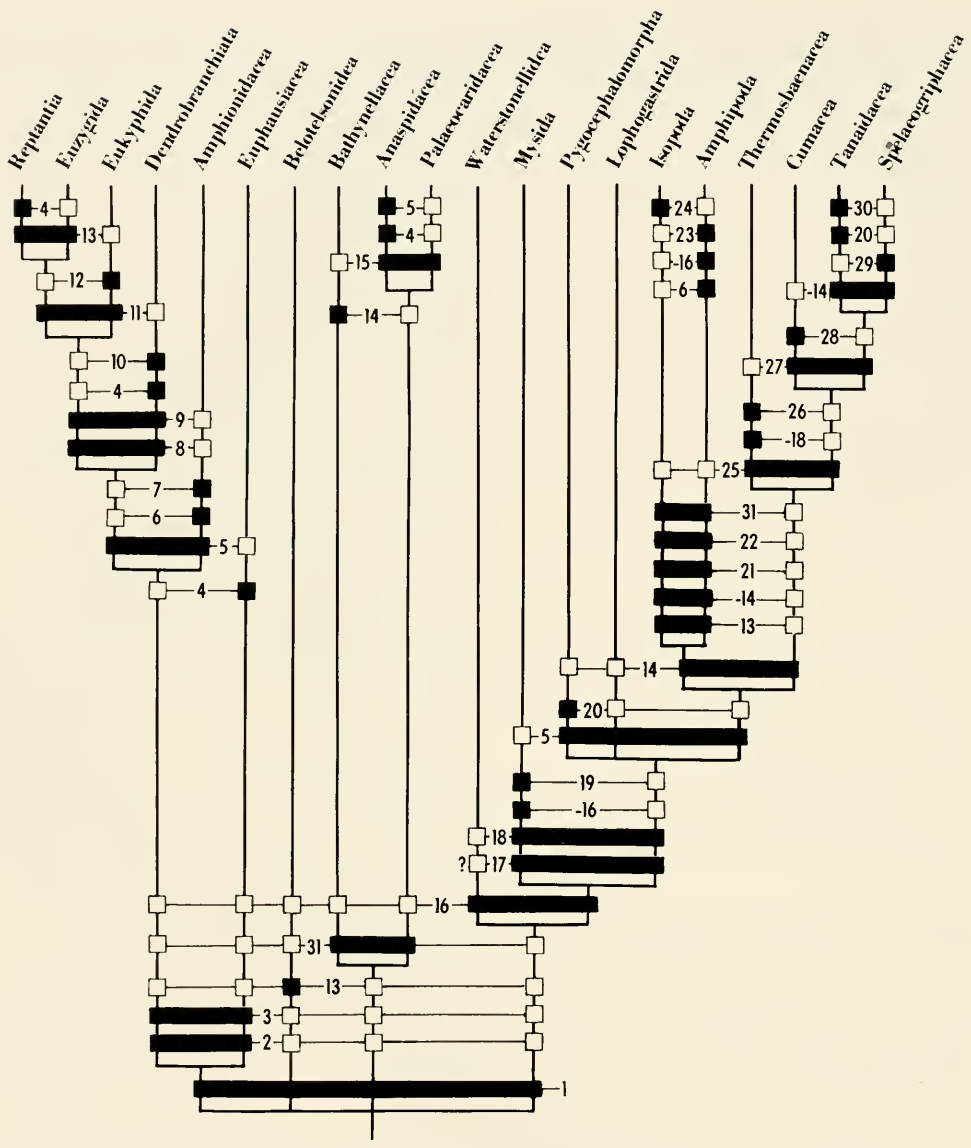

FIGURE 1. Cladistic relationships of component taxa of the Eumalacostraca, the presence of a carapace considered primitive. This is the shortest cladogram with the lowest homoplasy value, the base of the cladogram with an unresolved quadrochotomy between eucarids, belotelsonids, syncarids, and waterstonellids/peracarids. □ primitive, ■ derived.

nellidea and the "peracarid" line above Mysida. Wagner 78 is designed to produce the best resolved cladogram possible from the data given and, thus, the preferred version is that seen in Fig. 1. If on the other hand we wish to tolerate a slightly greater degreee of uncertainty (Schram, 1983), then we may choose the variant of Fig. 2 in which peracarids can be recognized as a distinct lineage. The relationships indicated in Figure 1, however, are not without considerable biological interest. The thrust of the early evolution of the waterstonellid/peracarid line was towards increasing specialization of thoracopods. First the primitive respiratory epipodites were lost, then oöstegites and maxillipedes were evolved, and finally some further specializations occurred in specific lineages such as filtratory endopods in mysidans (Attramadal, *pers. comm.*), and further maxillipedal and ambulatory modifications in pygocephalomorphs (Schram, 1974).

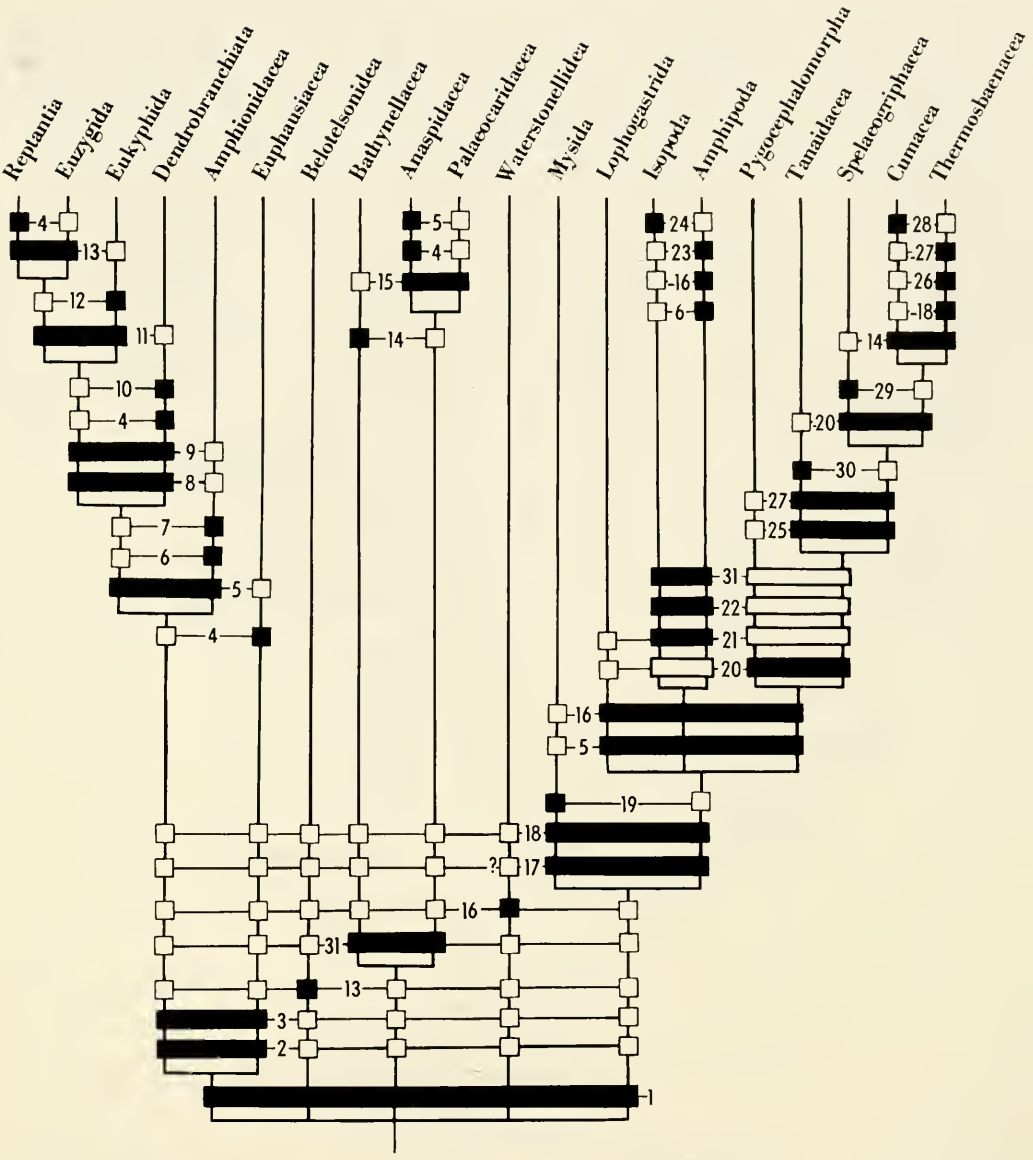

FIGURE 2. Cladistic relationships of component taxa of the Eumalacostraca, the presence of a carapace considered primitive. A variant cladogram from that of Fig. 1 exhibiting (1) unresolved quintichotomy at the base that allows a separation of waterstonellids and peracarids (which would shorten the tree, not involve any change in the number of convergences over that of Fig. 1, but would inject a higher level of uncertainty into the cladogram) and (2) an association of pygocephalomorphs as a sister group of the brachycaridans (which would not involve a lengthening of the cladogram but would inject one extra character reversal over that seen in Fig. 1). □ primitive, ■ derived.

Several interesting points emerge from these analyses. Many of the more-or-less controversial higher taxa (Cohorts and Orders) of Schram (1981), emerge, viz., Hemicaridea (Cumacea, Tanaidacea, and Spelaeogriphacea), Brachycarida (Hemicaridea and Thermosbaenacea), Eucarida (Euphausiacea, Amphionidacea, and Decapoda), and Acaridea (Isopoda and Amphipoda). The latter also seems to bear some relationship to a yet unnamed new order being proposed by T. Bowman, R. Hessler, and H. Sanders which, interestingly, seems to fill one of the "unoccupied" *Baupläne* of Schram (1981). On the other hand, some taxa derived from Schram (1981) do not seem viable: e.g.,

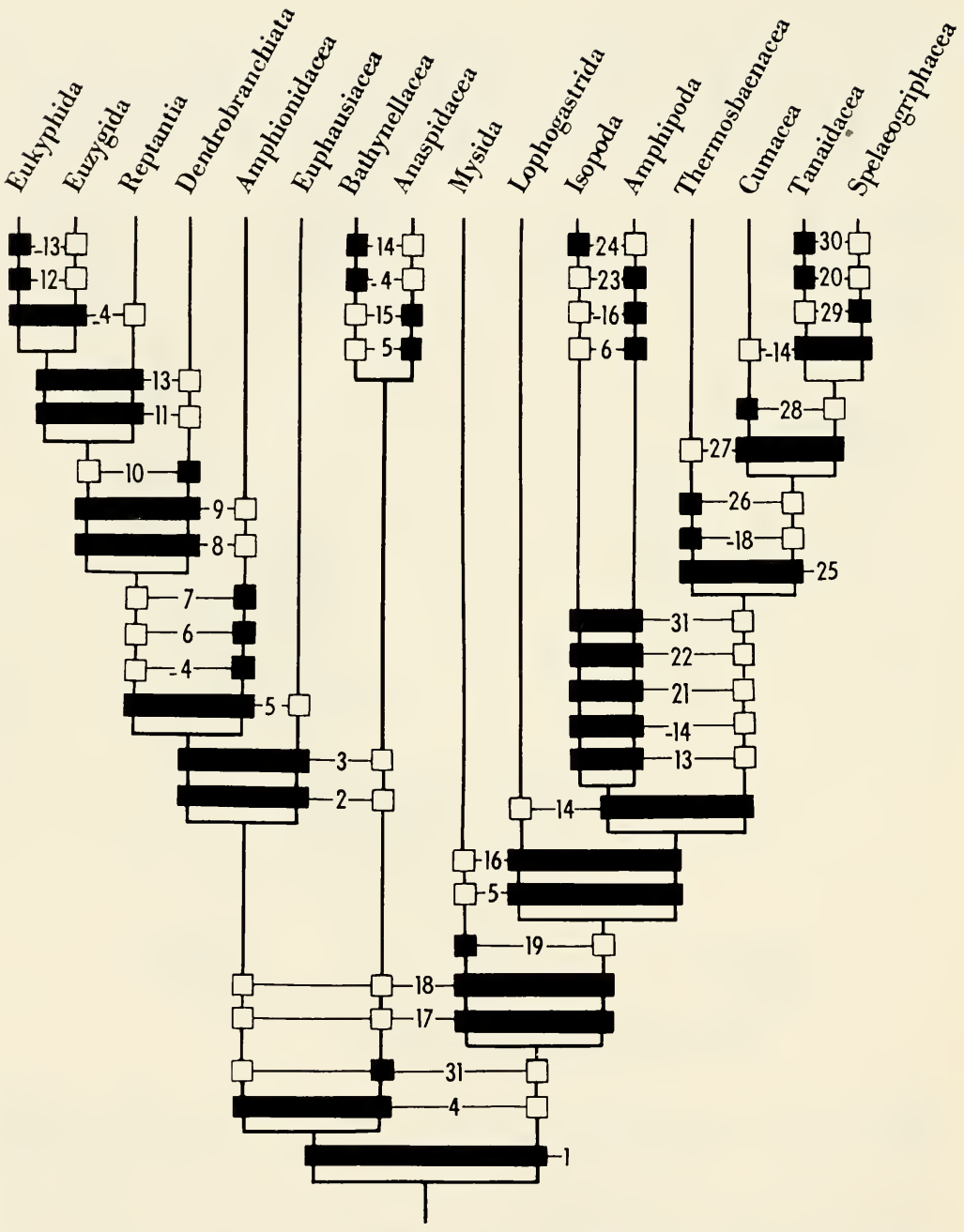

FIGURE 3. Cladogram based on the same character data as that used in cladograms of Figure 1, but analyzing only living groups and excluding the 4 extinct taxa, Palaeocaridacea, Belotelsonidea, Waterstonellidea, and Pygocephalomorpha. □ primitive, ■ derived.

Arthrostraca in the sense of Haeckel (1896), Giesbrecht (1913), or Grobben (1919) which unites all carapaceless syncarid and acaridean forms; or Mysoida (Belotelsonidea, Mysidacea, and Waterstonellidea), which seems invalid as a cladistic or taxonomic unit.

I decided to test the effect on the overall scheme of relationships when the fossil taxa were excluded from consideration (Fig. 3). Little change was noted except to ally

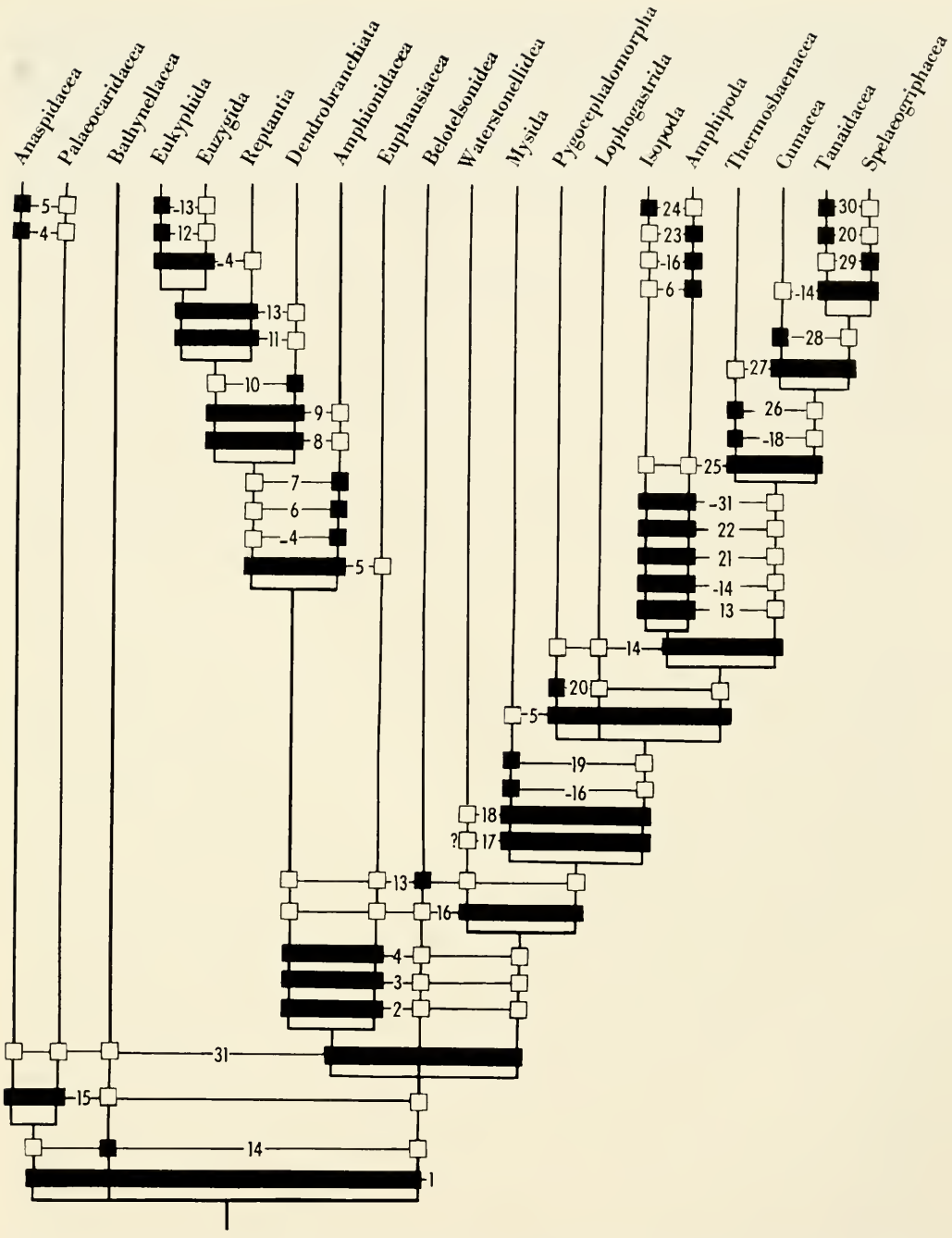

FIGURE 4. Cladogram with all taxa and character data the same as in Fig. 1, except the scoring of character 31 is reversed and the presence of a carapace is treated as a derived feature, as favored by Dahl (1983). □ primitive, ■ derived.

syncarids and eucarids as sister groups. Some slight modifications occurred in the arrangement of higher eucarids, but otherwise the basic relationships of the taxa of Fig. 1 are preserved. The total homoplasy value (a measure of the amount of convergence) is somewhat higher (388 vs. 372) in the non-fossil scheme than in that which includes the extinct groups, although the total length of both trees is not that much different, 44 without fossils as opposed to 46 with extinct groups included.

I also tested the contention of Dahl (1983) that the carapace is a derived feature, the lack of a carapace being viewed as primitive (Fig. 4). This test resulted in a somewhat longer cladogram than those in Figure 1 (47 vs. 46), but one which has a dramatically higher total homoplasy value (510 vs. 372). Similar results were obtained when the data based on Dahl's concept were run without extinct taxa. It would seem, therefore, that the suggestion by Dahl that the carapaceless state is the primitive one for eumalacostracans engenders a more complicated and less parsimonious array of relationships. Note, however, that the relationships within peracarids persist, including that of breaking apart Mysidacea.

Discussion

Characters difficult to use

Certain characters were deliberately not used here though they have found widespread employment in the taxonomy and phylogenetic discussions of Eumalacostraca by various authors.

In eucarids, although the structure of maxillipedes was used (lamellate appendages with endites directed mediad), the number of them was not (three maxillipedes and thus the name decapod). The anatomical and functional state of thoracopods in higher eucarids is actually more varied than one would be led to believe from the automatic connotation engendered by the term "decapod." In several instances, e.g., many Dendrobranchiata, the so-called third maxillipede is actually more "pediform" in structure and function than "maxillipediform." Also, certain "pereiopods" actually have little locomotory function but are utilized in food acquisition and processing as well as defense. For example, in euzygids (=stenopodids) the fourth and fifth thoracopods are chelipedes and directed anteriad towards the mouth field resulting in a hexapodous condition instead of a decapodous one in these animals. In astacideans the characteristic great chelipedes of the fourth thoracopods serve in food procurement and defense, making the animal functionally octopodous. So while there are good maxillary and maxillipedal features which can serve to delineate a taxon Decapoda, ironically true decapody is not a particularly good character to assist in such delineation.

Another feature taken for granted in discussion of eumalacostracan evolution is the fusion of the first thoracomere to the cephalon. Bathynellacea, of course, do not have this fusion. The Carboniferous genera *Belotelson* and *Waterstonella* apparently had free first thoracomeres as well, as they lacked maxillipedes altogether. Hence, it is imperative to resolve whether or not all living forms with a carapace do or do not fuse the first thoracomere to the head. For example, euphausiaceans lack a maxillipede, have the carapace fused to the thoracomeres, but have all thoracomeres associated together separate from the maxillary segment. Examination of mysidaceans revealed a variable state of affairs. Lophogastridans, with their well-developed maxillipedes, closely associate the first thoracomere with the cephalon and separate it from the second and following thoracomeres. However, in the mysidan *Neomysis americana* there is a separation of the maxillary from the thoracic segments, with all eight sets of thoracopods closely associated and separated by a distinct skeletal bar from the more anterior mouthparts. So in mysidans the first thoracomere is clearly not fused to the cephalon, although there is a tendency to develop maxillipedes. This feature serves to break apart the taxon Mysidacea, making Mysida a sister group to all other peracarids.

I also excluded three characters which have been asserted as distinctly peracaridan, including the lacinia mobilis mentioned above. The presence of a manca *stage* is frequently cited as a characteristic of peracarids. Generally workers used this feature as if they were dealing with a manca *larva*. Mancas, however, are not to be equated with the zoea, cypris, or other larval types which have considerable cladistic merit (see for example character 2). A "manca" is a stage of development which can have various forms of expression (Newman 1983). Amphipods are generally said to lack a manca, yet some hyperiids are freed from the female in a virtual manca state (Laval 1980). Some adults express a permanent manca condition, e.g., the genus *Thermosbaena*.

Manca stages also occur outside the peracarids, e.g., bathynellaceans hatch in an extreme "mancoid" condition lacking several of the posterior thoracopods and in the adults of some forms the last thoracopod can be missing or greatly atrophied. The presence or absence of a manca may be better understood in terms of constraints placed on development by egg size (e.g., Steele and Steele 1975). Characters of marsupial and maxillipedal form alone can be used to delineate peracarids more securely; and while the presence of a manca stage may assist in this delineation, it is not as unambiguous as one would suppose.

The same observation can be made of the monocondylic coxa/basis articulation recently noted by Hessler (1982). This character might appear to be a useful congruent feature towards establishing a concept of Peracarida. However, it has a variety of expression difficult at this time to evaluate. For example, the monocondyle variously arises from positions that are either lateral (tanaids), purely posterior (*Spelaeogriphus*), or postero-lateral (all other peracarids). Nor do all thoracopods have this joint. In tanaids the third through fifth limbs have a dicondylic joint whereas only the sixth through eighth have the distinct monocondyle. Completely aberrant condyle, muscle, and/or joint arrangements are seen in amphipods and mysidaceans. These latter two groups also display different degrees of expression of these features throughout the whole thoracopodal limb series. Although coxal/basal structure seems to second peracarid monophyly, problems with variety of expression and assessment of polarities between these variations preclude its use here.

Characters rejected for use

Two suites of traditional characters were completely rejected, viz., those of gut structure and embryo flexion which have played so prominent a role in the work of Siewing, and which resulted in the diametric separation of isopods and amphipods. The more that is discovered about gut morphology, the more it seems that the digestive system is too plastic to yield any useful data for phylogenetic analysis. Kunze (1981, and *personal communication*) has noted that the anatomy of the stomach of isopods is closely tied to feeding habits. Ide (1892) and Naylor (1955) provided details of gut structure in *Idotea* identical to that supposedly characteristic of amphipods, including an anteriorly directed mid-dorsal caecum in *I. tricuspidata*. Carol Diebel (*pers. comm.*) is finding that stomach structure among hyperiid amphipods is so diverse as to be uncharacterizable because of adaptations to particular feeding strategies.

The other character rejected here, but given great weight by Siewing, is whether the developing embryo is flexed ventrally or dorsally within the egg membranes. First, few studies within and between groups of peracarids have been performed to determine the distribution of these states. Second, one of these flexures must be primitive and the other advanced. As such, only one of them can be used to characterize one of the groups which possesses it, but they are not both derived characters. It might appear that the dorsal flexure is derived, but insufficient data exist from within and without peracarids in order to assess polarity. And third, flexure in embryos seems better understood in terms of the mechanics of a particular developmental sequence rather than in terms of phyletic trends. Note that in forms with a ventral flexure, there is typically a very distinct egg–nauplius stage in early development, the development of the teloblasts lags behind that of the primary part of the head. The development of a caudal papilla and a caudal furrow which lead to ventral flexure is thus possibly related to the rapid development of the naupliar region. In contrast, in animals with a dorsal flexure, the appearance of the naupliar anlagen lags. In such forms the teloblasts not only appear early in the sequence of events around the blastopore, they initiate their divisions early such that the naupliar and anterior metanaupliar somites appear virtually simultaneously. It would appear that because of the slower head development the proliferation of body somites is allowed to occur along the entire ventral and posterior surfaces of the egg without the appearance of a caudal furrow or papilla to produce ventral flexure. Clearly the "phylogenetic power" of the apparent differences of flexure between isopods and amphipods has been somewhat overextended.

Variant cladograms

Two variants in the cladograms were produced by the program frequently enough to require some comment here. One is a variation in the higher decapods seen in Figures 1 and 3. In one (Fig. 1), somewhat more parsimonious, eukyphids are placed as a sister group to euzygids and reptants. In the other (Fig. 3), reptants are a sister group of euzygids and eukyphids. The former is a more traditional arrangement, but the latter is all the more startling in light of the pregnant comment of Felgenhauer and Abele (1983) that it was their belief that the origins of the so-called "natant" groups of decapods ". . . are to be found among those groups traditionally considered reptants."

Indeed the entire issue of relationships within the decapods is under intense study right now. Burkenroad (1981), using branchial and ontogenetic characters not employed in this analysis, essentially obtained an arrangement of taxa like that seen in Figure 3. However, Felgenhauer (*personal communication*) is examining various features of external and internal anatomy of natant forms in an attempt to arrive at an assessment of cladistic relationships within decapods. For these reasons, it may be wise to avoid use of terms like Decapoda and/or Pleocyemata for the time being, and rather treat the taxa within Eucarida as one long transition series.

Another notable variant is seen in the higher peracarids between Figs. 1 and 2. The scheme in Fig. 2 is slightly less parsimonious, but if one can tolerate the additional character reversal it entails, then the arrangement is a sequence of events which is of considerable biological interest. The isopod/amphipod line seems to represent one in which the thrust of the radiation is toward varied exploitation of food resources because of the great plasticity in gut structures. The brachycaridan line, especially when the pygocephalomorphs are associated with it, seems to be a line which represents exploitation of reproductive strategies. Both pygocephalomorphs and tanaids have cones on the males. The supposed seminal receptacles mentioned by Brooks (1962) on pygocephalomorphs bear little actual resemblance to such structures. These structures are more likely large genital cones on the eighth thoracic sternites of males. The brachycaridan line is generally characterized by respiratory specializations of the maxillipedes and thoracopods. It is also a transition series in which carapace, pleopods, and the oöstegite brood pouch are reduced or lost, culminating in the condition seen in the thermosbaenaceans. Insofar as the component taxa are currently understood, this line also exploits reproductive and unusual sexual strategies that maximize the number of offspring from any one generation (e.g., see Sieg 1983, for tanaidaceans, or Corey 1981, for cumaceans).

Conclusions

Several conclusions can be drawn concerning the analyses made here:

1) At least in part, the taxonomic scheme for the Eumalacostraca suggested by the identification of *Baupläne* within the group (Schram 1981) is supported, especially in regards to peracarid types. The idea of a taxon Arthrostraca is not favored, but the reassociation of isopods with amphipods in the sense of the old taxon Edriophthalma, and the linking of short carapace forms, does have some merit.

2) If some degree of uncertainty is accepted, then the relationships within Peracarida postulated by Siewing (1951, 1956) can be subscribed to, but only if considerable multiple convergences can be tolerated within a distinctly unparsimonious scheme.

3) The concept of the carapace as a derived feature in the sense of Dahl (1983) is acceptable only by tolerating a great many more convergences than occur when the presence of a carapace is viewed as primitive.

4) The concept of a formal taxon Mysidacea seems best abandoned. The three subtaxa traditionally placed within it (Lophogastrida, Mysida, and Pygocephalomorpha) are distinct from each other regardless of whether the presence of a carapace is considered primitive or derived.

What taxonomy of Eumalacostraca should be derived from all this? The eucarids are destined for some kind of realignment, especially of the higher taxa. The phylo-

genetic integrity of the brachycaridans is stable enough, whether or not pygocephalomorphs are closely associated with them. The resolution of relationships within the edriophthalman branch must await the description and evaluation of the new order of Bowman, Hessler, and Sanders, as well as a reevaluation of relationships within isopods and amphipods using a careful analysis of character states in all subgroups therein. In regards to the latter, we may resurrect the old taxon Laemodipoda, wherein caprellids and cyamids are separated as sister groups off by themselves. Such a study is currently under way.

It is my intent here to point out two things. First, there is merit in carefully reflecting on what are the constituent structural plans expressed within any particular taxon, alert to the fact that any particular *Bauplan* may or may not be developed, or may or may not be the basis of an extensive radiation. Second, regardless of the ongoing philosophical and in large part tautological debate on taxonomic theory, we must make some organized careful evaluations of characters and what their condition and polarity might be throughout *all* members of a group. These are problems which have been all too often neglected in the history of crustacean studies, but are not unique to the study of these arthropods.

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Literature Cited

Brooks, H. K. 1962. The Paleozoic Eumalacostraca of North America. Bulletins of American Paleontology 44:163–338.

Burkenroad, M. D. 1981. The higher taxonomy and evolution of Decapoda. Transactions of the San Diego Society of Natural History 19: 251–268.

Calman, W. T. 1904. On the classification of Crustacea Malacostraca. Annals and Magazine of Natural History (7)13:144–158.

———. 1909. Crustacea. *In* R. Lankester (ed.). A Treatise on Zoology. Vol. VII. Adam & Charles Black, London.

Corey, S. 1981. Comparative fecundity and reproductive strategies in seventeen species of Cumacea. Marine Biology 62:65–72.

Dahl, E. 1983. Malacostracan phylogeny and evolution. Crustacean Issues 1:189–212.

———, and R. R. Hessler. 1982. The crustacean lacina mobilis: a reconsideration of its origin, function, and phylogenetic implications. Zoological Journal of the Linnean Society, London 74:133–146.

Felgenhauer, B. E., and L. G. Abele. 1983. Phylogenetic relationships among shrimp-like decapods. Crustacean Issues 1:291–312.

Fryer, G. 1964. Studies on the functional morphology and feeding mechanism of *Monodella argentarii*. Transactions of the Royal Society of Edinburgh 66:49–90.

Giesbrecht, W. 1913. Crustacea. *In* Handbuch der Morphologie der Wierbellosen Tiere. Bd. 4. Arthropoden. Jena: Gustav Fisher.

Grobben, K. 1919. Über die Musculatur des Vorderkopfes der Stomatopoden und die systematische Stellung dieser Malakostrakengruppe. Sitzungberichte der Akademie Wissenschaften, Wien 128:185–214.

Haeckel, E. 1896. Systematische Phylogenie: 2 der Wirbellose Thiere. Georg Reimer, Berlin.

Hessler, R. R. 1969. Peracarida. Pp. R360–R363 *in* R. C. Moore (ed.). Treatise on Invertebrate Paleontology, Part R., Arthropods 4, Vol. I. Geological Society of America and University of Kansas Press, Lawrence.

———. 1982. The structural morphology of walking mechanisms in eumalacostracan crustaceans. Philosophical Transactions of the Royal Society, London (B)296:245–298.

———. 1983. A defense of the caridoid facies: wherein the early evolution of the Malacostraca is discussed. Crustacean Issues 1:145–164.

Ide, M. 1892. Le tube digestion des Edriophthalmes; etude anatomique et histologique. Cellule 8:97–204, plates 1–7.

Kunze, J. C. 1981. The foregut of malacostracan Crustacea: functional morphology and evolutionary trends. American Zoologist 21:968.

Laval, P. 1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous

zooplankton. Oceanography and Marine Biology Annual Review 18:11–56.
Naylor, E. 1955. The diet and feeding mechanism of *Idotea*. Journal of the Marine Biological Association of the United Kingdom 34:347–355.
Newman, W. A. 1983. Origin of the Maxillopoda: urmalacostracan ontogeny and progenesis. Crustacean Issues 1:105–120.
Schram, F. R. 1974. Convergences between Late Paleozoic and modern caridoid Malacostraca. Systematic Zoology 23:323–332.
———. 1981. On the classification of Eumalacostraca. Journal of Crustacean Biology 1:1–10.
———. 1983. Method and madness in phylogeny. Crustacean Issues 1:331–350.
Sieg, J. 1983. Evolution of Tanaidacea. Crustacean Issues 1:229–256.
Siewing, R. 1951. Besteht ein engere Verwandschaft zwischen Isopoden und Amphipoden. Zoologisches Anzieger 147:166–180.
———. 1956. Untersuchungen zur Morphologie der Malacostraca. Zoologisches Jahrbuch, Abteilung Anatomie 751:39–176.
Steele, D. H., and V. J. Steele. 1975. Egg size and duration of embryonic development in Crustacea. Internationale Revue der gesamten Hydrobiologie 60:711–715.
Watling, L. 1981. An alternative phylogeny of peracarid crustaceans. Journal of Crustacean Biology 1:201–210.
———. 1983. Peracaridan disunity and its bearing on eumalacostracan phylogeny with a redefinition of eumalacostracan superorders. Crustacean Issues 1:213–228.

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History and status of the avifauna of Isla Guadalupe, Mexico

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Abstract. Since 1954, renewed interest in Isla Guadalupe, stimulated by the research of the late C. L. Hubbs, has resulted in much new information on the avifauna. In this paper we review the status of the birdlife through 1982, provide an historical review of the research, including information on the timing and extent of the many expeditions, and provide a bibliography.

Resumen. Desde 1954, interés renovado en la Isla Guadalupe, promovido por las investigaciones del Dr. C. L. Hubbs, ha resultado en mucha nueva información sobre la avifauna. En esta presentación detallamos lo conocido sobre la historia natural de los aves hasta 1982, damos un resumen histórico sobre las investigaciones, incluyendo información sobre el estacionamiento y duración de las expediciones y ofrecemos una bibliografía.

Introduction

Because of its unique plant and animal life, Isla Guadalupe, Mexico, has fascinated biologists since the time of its scientific "discovery" in 1875. This rugged and remote volcanic island, 220 miles south of the Mexico–United States boundary and 160 miles west of the peninsula of Baja California, was the home of ten endemic species or subspecies of birds (an eleventh has recently been proposed). But the history of the birdlife "is a sad one of reduction and extermination through destruction of habitat by feral goats, predation by introduced house cats, and regrettably, some excess of zeal by collectors" (Howell and Cade 1954: see also Huey 1924, 1925), and many of the endemics are gone.

Much has been written about the avifauna, and the history of some of the extinct forms has been well documented. Ridgway (1876), Bryant (1887*a*), Thayer and Bangs (1908) and Hanna (1925) provided comprehensive reviews of the birdlife and these were made current by Howell and Cade in 1954. Since then, sufficient new information has been obtained to prompt a further compilation.

For a description of the island and its general ecological settings and geology see Howell and Cade (1954), Lewis (1971), and Johnson (1953). A good summary is provided by Lindsay (1966:2); who wrote: "Guadalupe Island is about 22 miles long from north to south, and four to six miles wide over most of its length. The highest part is at the north end, where magnificent sheer cliffs tower over the sea or narrow beaches of cobbles and sand. The central part is a plateau sloping toward the south end, but the whole island is very rugged. Most of the base rock is red lava, and several of the lesser peaks are cinder cones. Recent research has shown that the oldest lava flows occurred about 7,000,000 years ago."

Most of the island is devoid of vegetation. A remnant of a formerly large cypress

forest (*Cupressus guadalupensis*) about 1½ miles long, is located in the north central part of the island. The endemic fan palm (*Erythea edulis*) is fairly common on the north slope of the island, and atop the main ridge at the north end there are stands of Island Oaks (*Quercus tomentella*) and Guadalupe Island Pines (*Pinus radiata* var. *binata*). The highest peak, Mount Augusta, rises more than 4200 feet above the sea. A map of the island, with names of major localities, is given in Figure 1.

History of Ornithological Research

The Hungarian explorer Johan Xántus de Vesey is generally acknowledged as having been the first naturalist to visit the island. He was becalmed there on 17 March 1859, while en route between San Francisco and Cabo San Lucas (Madden 1949). In his journals Xántus described several species of birds whose identity might be inferred. Yet, his accounts of the island itself are at such variance with those of an earlier French expedition (duPetit-Thouars 1956) that they undermine the credibility of his reports, and we have given them no attention.

It was the work of the botanist Edward Palmer that drew first attention to the island. Palmer, collecting plant specimens for the U.S. National Museum, arrived in 1875, intending to remain for six weeks (Blake 1961). Instead he found himself stranded for four months (Table 1), which afforded him ample time to collect eight of the nine endemic taxa of landbirds, all of which were quickly described by Robert Ridgway (1876).

Palmer's visit came just in time, for the island was already undergoing a series of rapid and irreversible changes. Goats had been introduced as a source of meat by sealers or mariners, perhaps as early as the 18th century, and more were introduced for a commercial wool-producing enterprise in the 1870s (*San Diego Union,* 15 March 1873; Anon. 1874). They numbered in the tens of thousands by the time of Palmer's visit, caused the elimination of much of the island's vegetation (already noted by the French in 1838), and forced much of the birdlife to be concentrated in the few wooded areas.

Spurred by Palmer's discoveries, Walter E. Bryant spent a short time on the island in January 1885, then returned in December with the intention of spending six weeks there. Three and a half months elapsed before his ship returned. Palmer's work had

Table 1. Chronology of ornithological research at Guadalupe Island, 1875–1953.

Observers		Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec	References
Palmer	1875	▬▬▬▬	Blake 1961
Bryant	1885	?	Bryant 1887*a*
Bryant	1885–1886	▬▬▬▬ ▬	Bryant 1887*a*
Anthony, Streator	1892	▬	Anthony 1901, 1925
Gaylord, Anthony	1896	▬	Gaylord 1897
Anthony et al.	1897	▬ ▬	Davidson 1928, Kaeding 1905
Thoburn	1897	▬	Thoburn 1899
Beck	1900	▬	Abbott 1933
Hartert, Rothschild	?		Howell and Cade 1955
Brown et al.	1906	▬▬▬	Thayer and Bangs 1908
Townsend	1911	▬	Townsend 1911, 1923
Beck	1912	?	Abbott 1933
Anonymous	1913	▬	Kimball 1922
Anthony et al.	1922	▬	Anthony 1925, Hanna 1925
Huey	1923	▬	Huey 1924
Hanna et al.	1925	▬	McLellan 1925
Swarth	1932	▬	Swarth 1933
Walker	1938	▬	Huey 1954
Vanderbilts	1941	▬	Bond and deSchauensee 1944
Howell and Cade	1953	▬	Howell and Cade 1954

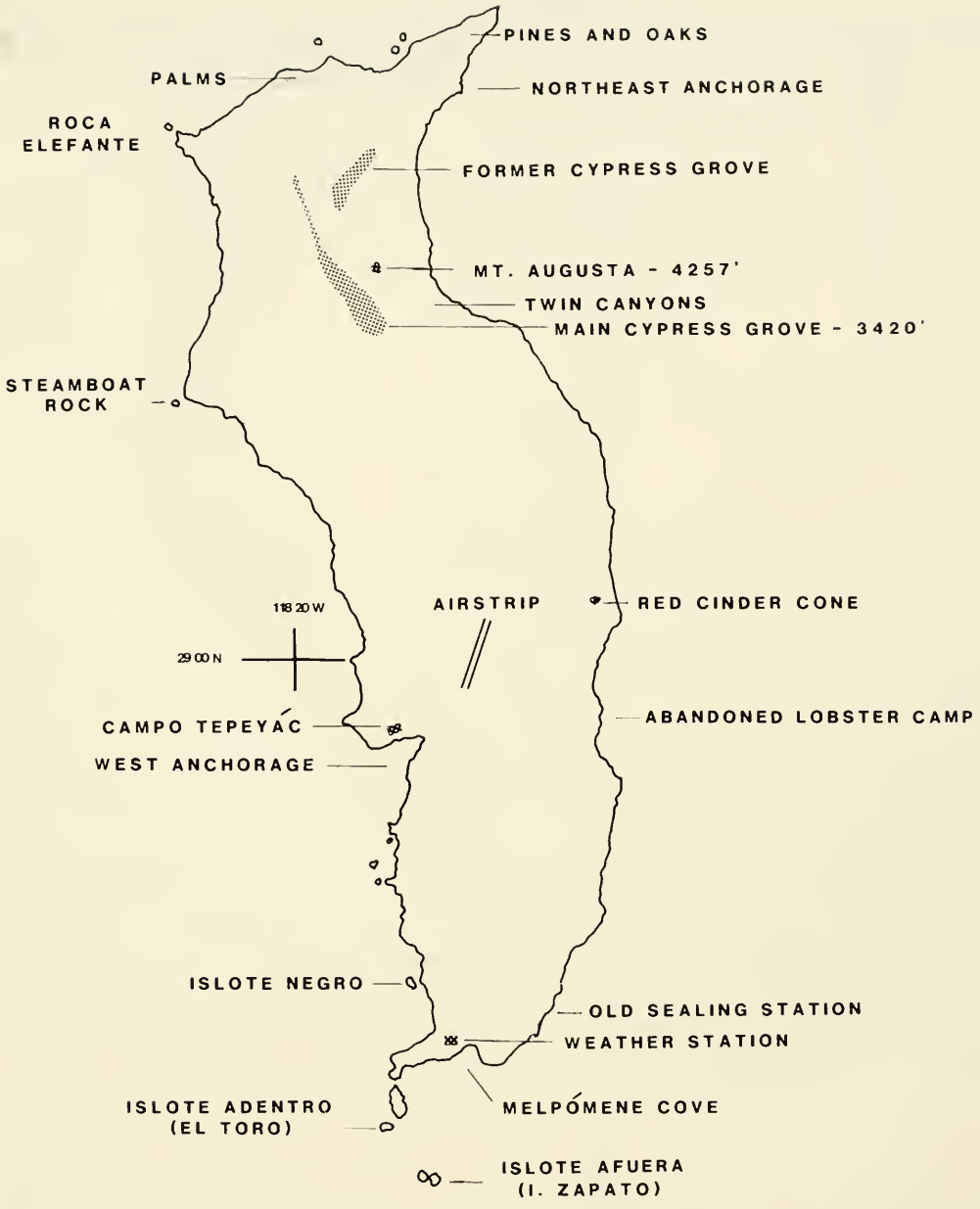

FIGURE 1. Isla Guadalupe, showing major localities and forested areas mentioned in this report.

been so thorough that Bryant was unable to discover any additional endemic landbirds, but he did amass a number of unusual observations (Bryant 1887*a*). More importantly, he discovered the Guadalupe Petrel (*Oceanodroma macrodactyla*), the first endemic seabird to be recognized (Bryant 1887*b*).

In the last decade of the 19th century, several expeditions made brief stops at Guadalupe. A. W. Anthony made several trips and was the first to report the destruction of biota by feral goats (Anthony 1901). Within a few years many of the endemic birds were extinct. The last report of a Guadalupe Caracara (*Polyborus plancus lutosus*) was made by Rollo Beck, who collected nine in December 1900. An expedition from the

TABLE 2. Expeditions to Guadalupe Island by C. L. Hubbs.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total days
1946								■					2
1950		■											8
1954											■		8
1955						■							7
1956								■	■				5
1957		■		■						■		■	26
1958				■									9
1960		■											6
1963				■									9
1964											■		6
1965			■										7
1966				■									8
1967				■									9
1969		■											5
1970	■			■									12
1971					■								6

Thayer Museum, including W. W. Brown, spent two months on the island in the spring of 1906. After scouring the island, they declared the Guadalupe Wren (*Thryomanes bewickii brevicauda*) and Guadalupe Towhee (*Pipilo erythrophthalmus consobrinus*) extinct (Thayer and Bangs 1908), and predicted the quick demise of the Guadalupe Flicker (*Colaptes auratus rufipileus*). Yet, despite intense predation by cats, the Guadalupe Petrel persisted "in large numbers." Only six years later, however, in 1912, Beck collected two downy chicks, the last known examples (Davidson 1928).

After the basic collections had been made, and the extinction of the endemics had been documented, interest in the island lagged. Some ornithologists continued to visit it (often en route to more exciting localities) in the 1920s and 1930s (e.g., Hanna 1925), but little new information resulted.

Commencing in the 1940s and continuing through the early 1970s studies by Carl L. Hubbs and his many colleagues renewed interest in Guadalupe. Between 1946 and 1971, Hubbs made 21 expeditions to the island (Table 2). Hubbs discovered that small islets at the southern end of the main island were important seabird colonies. In addition to initiating population studies on seabirds, he reported the apparently distinctive summer and winter populations of Leach's Storm-Petrels (Hubbs 1960) that have received much subsequent attention (Crossin 1974, Ainley 1980, 1983, Bourne and Jehl 1982). He also discovered the only known fossil locality on the island (Pleistocene), which has yielded the remains of a few seabirds (Hubbs and Jehl 1976).

In 1953, T. R. Howell and T. J. Cade spent five days on the island, on one of Hubbs' expeditions. Their findings (Howell and Cade 1954, 1955) resulted in the first discussion of the birdlife in several decades. Additional work by the Pacific Ocean Biological Survey Program (POBSP) in the late 1960s and early 1970s (DeLong and Crossin MS, Brownell MS, Crossin MS, 1974) revealed much about the nesting seabirds.

Since the late 1960s we have each had occasion to visit Guadalupe several times. Our observations, and those of many other biologists who have generously contributed data (Table 3), and the voluminous field notes of the late Carl L. Hubbs provide the basis for this report. Note, however, that as with earlier studies nearly all of the recent work has been concentrated in late winter through early summer and that the fall season, with one exception, is unrepresented. We have attempted to make the report comprehensive and current, and to provide a complete ornithological bibliography. This compilation was stimulated in part by a request, for planning purposes, from the Mexican government, through Dr. Martín Gonzáles. Because prospects of additional surveys in 1982 and 1983 failed to materialize, we are making the report available now. We acknowledge, however, that much remains to be learned before our knowledge of the present avifauna is adequate.

Table 3. Recent ornithological observations on Isla Guadalupe, Mexico.

Year	Month	Observers
1965	27–31 Jan	K. L. Kenyon
1967	26, 27, 30 Apr, 1–4 May, 21–24 Oct	R. L. DeLong and R. S. Crossin
1968	17–22 Apr, 20–23 Jun, 28–29 Jun	R. L. Brownell, R. S. Crossin, R. L. DeLong
1969	21–23 Feb	J. R. Jehl, Jr.
1970	19–27 Jan, 12–18 Apr	J. R. Jehl, Jr.
1971	15 Mar, 17–23 May	J. R. Jehl, Jr.
1972	mid Dec	K. Briggs
1973	22 Nov–26 Dec	E. Mirsky
1975	12–13 Jul	J. R. Jehl, Jr.
1977	20 Jun–13 Jul	M. Pierson and M. Riedman
1978	9–20 Feb 16 Apr 17–18 Dec	M. Pierson, E. Chu et al. W. T. Everett K. Briggs
1979	24 Mar, 18 Apr	W. T. Everett
1980	4–5 May	W. T. Everett
1981	19–26 Aug	D. Duncan
1982	12–15 Feb, 4–6 Mar	R. Condit

Annotated List of Species

In the following section we provide synoptic information on all species of birds recorded on Guadalupe Island and in waters immediately adjacent (within approximately 15 km) of the island. We include information on many species of seabirds, which were not considered by Howell and Cade (1954). Nomenclature follows the AOU Check-list (1983), except for *Pluvialis fulva* (see Connors 1983). The following abbreviations are used: AMNH, American Museum of Natural History; CAS, California Academy of Sciences; HSWRI, Hubbs-Sea World Research Institute; LACMNH, Los Angeles County Museum of Natural History; SDNHM, San Diego Natural History Museum; UCLA, University of California Los Angeles.

Arctic Loon (*Gavia arctica*)

Uncommon winter visitor. Palmer found an adult washed ashore on 20 May 1875 (Ridgway 1876). Hubbs collected one on 13 February 1957 and saw two others on his expedition (8–15 February 1957), and Mirsky (MS) observed one on 23 November 1973.

Pied-billed Grebe (*Podilymbus podiceps*)

Accidental. Hubbs collected one on 27 October 1957; location of specimen unknown.

Eared Grebe (*Podiceps nigricollis*)

Considered accidental by Howell and Cade (1955) on the basis of a specimen reported by Rothschild and Hartert (1902). There are four subsequent reports. Hubbs

FIGURE 2. Guadalupe Storm-Petrel (*Oceanodroma macrodactyla*). Photograph of a mount in the Field Museum of Natural History, Chicago.

collected two on 12 February 1957 (LACMNH) and reported taking another on 30 October 1957; Mirsky (MS) reported one on 23–25 November 1973.

Western Grebe (*Aechmophorus occidentalis*)

Accidental. Two reports by Hubbs of single birds on 12 November 1954 and 17 December 1957.

Short-tailed Albatross (*Diomedea albatrus*)

Probably regular in the area until the late 19th century. Bryant (1889) reported five between Ensenada and Guadalupe in April 1886. Now very rare and not reported in Baja California for many decades.

Black-footed Albatross (*Diomedea nigripes*)

Uncommon but regular near the island through most of the year, with many sight records from September to June.

Laysan Albatross (*Diomedea immutabilis*)

This species is a rare but regular wanderer to Baja California. R. Wisner observed a single bird about 3 km off the north end of the island on 22 April 1958, and R. Pitman saw one 90 km to the northeast on 4 January 1980. Anthony (1898*b*) took a specimen between San Gerónimo and Guadalupe islands in March 1897.

Northern Fulmar (*Fulmarus glacialis*)

Irregular visitor in winter. Mirsky (MS) reported one on 6–7 December 1973. This species reaches the latitude of central Baja California in flight years.

Cook's Petrel (*Pterodroma cookii*)

This species occurs regularly off the coast of Baja California (Jehl, *pers. obs.*). Two were seen on 11 April 1961, 100 km north of the island (Small 1961). Pitman saw one along with another unidentified *Pterodroma* within 15 km of Guadalupe on 11 October 1979.

Pink-footed Shearwater (*Puffinus creatopus*)

According to Grinnell (1928): "First definitely recorded by Gaylord . . . as seen by A. W. Anthony near Guadalupe Island, September 17, 1896." While this record may be correct—the species is a common migrant nearer shore—we suspect that it more likely pertains to the Black-vented Shearwater, which breeds locally.

Sooty Shearwater (*Puffinus griseus*)

Probably a regular visitor from April to October. Thayer and Bangs (1908) reported taking two specimens "near" the island in June 1906, and Pitman saw one on 4 January 1979.

Black-vented Shearwater (*Puffinus opisthomelas*)

This shearwater has long been known to breed at Guadalupe. Anthony (1900) reported it to be "rather common . . . in several parts of the island, but in no place was there any large colony. Their nests were all inaccessible owing to the nature of the sites selected, whether in natural holes in the lava or under large boulders, and no eggs were secured. A night was spent on the top of the island in a heavy cypress growth, about 4000 feet above the sea. Here the shearwaters were heard all night, their choking, gasping notes coming from all sides as they flew through this grove."

Hubbs discovered and for many years surveyed the colony on Islote Negro, which in the late 1960s and early 1970s contained 100–150 pairs (Jehl, *pers. obs.*, Crossin MS, Brownell MS). Crossin visited Islote Afuera on 22–23 June 1968 and found a colony of 150+ pairs. We suspect that there may be other colonies on the main island because in the early evening flocks of 500–2500 shearwaters, too many to be accommodated by known nesting areas, stage at the south end of the island.

The breeding season at Islote Negro can be outlined with some confidence. By late November single birds begin to occupy burrows. By early January pairs are commonly found and fresh eggs are present by 5 March (Hubbs field notes). The peak of the egg-laying season occurs in early April, when most burrows contain an egg, but may extend to late June (Jehl, *pers. obs.*; Crossin MS). Young are present as early as late April and in late June most burrows have a chick. There are no data for later in the fall. Crossin reported that the phenology of the Islote Afuera colony was somewhat later than at Islote Negro.

Leach's Storm-Petrel (*Oceanodroma leucorhoa*)

There has been much uncertainty about the historical status of storm-petrels at Guadalupe, much of which may never be fully resolved because the early literature is inconsistent, and because cats have eliminated most, if not all, storm-petrel colonies on the main island, whose location and species composition cannot be fully reconstructed. The complicated case of the Leach's Storm-Petrel is best treated chronologically.

In the winter and spring of 1885–86, W. E. Bryant was stranded on Guadalupe for nearly four months. Near the end of his stay he discovered storm-petrels nesting

among the pines and cypress trees at the northern end of the island. Bryant (1887*a*) reported these as Leach's Storm-Petrels (*Oceanodroma leucorhoa*), and recognized that they had a more deeply forked tail and a longer middle toe than other races. Bryant (1887*b*) then named these as a new race (*O. l. macrodactyla*), the Guadalupe Storm-Petrel, which the AOU (1889) elevated to species rank.

In 1889, C. H. Townsend secured a single small storm-petrel, which had the sides of the rump "whitish," at sea near Socorro Island, 1200 km SE of Guadalupe. He described it as a new species (*O. socorroensis*), guessing that it nested at Socorro Island (Townsend 1890).

A. W. Anthony visited Guadalupe in May 1892 and collected three nestling Guadalupe Storm-Petrels, but did not mention other species. In 1896, Anthony and H. A. Gaylord visited Guadalupe in mid-September. Anthony spent a night atop the island but reported no petrels of any species (Anthony 1898*c*). However, Gaylord (1897) stated: "Regarding the Petrels which breed on the island, the hunters told us that while doing some stone work in the region of the Petrel colony, they had found two different species. They described the Guadalupe Petrel and an entirely black one, which together with a wing found on the trail to the cypress grove makes it appear that *O. homochroa* is an inhabitant of the island."

In late March, Anthony collected a series of adult *macrodactyla,* along with a few eggs. That summer he returned and collected young, noting that *macrodactyla* leaves the colony by 10 June. On neither trip did he find other species in the colony, but in June he collected a storm-petrel with enlarged ova at sea 120 mi north of Guadalupe, which became the type of Kaeding's Petrel (*Oceanodroma kaedingi*). This new form was distinguished by its small size and white rump, but Anthony (1898*a*) noted that there was much variation in rump color. From observations at sea, Anthony (1898*a*) surmised that the range of *kaedingi* extended from the Revillagigedos to southern California and guessed (1898*c*) that its breeding grounds were on Guadalupe. Also, he reidentified the wing ascribed to *homochroa* in 1896 as belonging to *kaedingi* (Anthony 1898*c*).

H. B. Kaeding (1905), who accompanied the 1897 expedition, was the first to allege a common breeding area for *kaedingi* and *macrodactyla.* He wrote that "the breeding grounds of *kaedingi* are as yet unknown, but it is probable that the birds occupy the burrows of Guadalupe Petrels . . . after the breeding season of the former is closed." In late May 1906, W. W. Brown and H. W. Marsden visited the breeding grounds of the Guadalupe Storm-Petrel (Thayer and Bangs 1908); they found *O. macrodactyla* but no other species.

By this time most of the islands off Baja California had been surveyed and taxonomists began to re-evaluate the variation in the Leach's Storm-Petrel group (including Swinhoe's Storm-Petrel, *O. monorhis,* of the western Pacific), a process that still continues (e.g., von Berlepsch 1906, Emerson 1906, Godman 1907–1910, Obserholser 1917, Loomis 1918, van Rossem 1942, Austin 1952, Todd 1955, Palmer 1962, Crossin 1974, Ainley 1980, 1983, Bourne and Jehl 1982, Power and Ainley MS). The work was made difficult because of the petrels' discontinuous breeding range, the scarcity of specimens from breeding colonies, the great variability in some populations, and the lack of knowledge about the location of breeding grounds. The last point was illustrated by A. C. Bent (1922), who reported that "Mr. Anthony wrote me that on Guadalupe Island the Guadalupe Petrels breed early, April 20 or earlier, and that after they are through breeding the Kaeding Petrels use the same burrows." As Anthony was the most knowledgeable ornithologist regarding the petrels of the region no one questioned his perpetuation of Kaeding's (1905) idea, even though all expeditions to the nesting grounds of *macrodactyla* failed to report any other species as nesting, and despite the fact that the nesting grounds of *kaedingi* had yet to be discovered (e.g., Oberholser 1917, Grinnell 1918).

On 11–17 July 1922 Anthony (1925) returned to Guadalupe and visited the nesting area of *macrodactyla.* That species had disappeared, but the expedition did find numerous bodies of *kaedingi* that had been killed by cats or were impaled on cholla, and

even found a week-old chick (CAS no. 25561). Unfortunately, no data were published on precise localities. Hanna (1925) stated that *kaedingi* "lived among the loose rocks and in holes in the cliffs," whereas Anthony (1925) said that it "evidently" nested in high cliffs at the north end of the island. Regardless, the discovery of the chick (i) provided the first proof that a species other than *macrodactyla* nested on the main island, (ii) established the island as a breeding location for *kaedingi,* (iii) is in accord with recent data that *kaedingi* is a crevice nester (*macrodactyla* nested in burrows in forested areas), and (iv) shows that Anthony had no evidence of burrow-sharing between *macrodactyla* and *kaedingi.*

In 1950, Carl L. Hubbs discovered and began to study the Leach's Storm-Petrels nesting on small islets at the south end of the main island. Hubbs (1960) was the first to recognize that there were evidently two populations, a larger form with white rump that bred in winter and fledged young by April, and a smaller form with less white on the rump that began laying in June and fledged young in October or November. Surveys by the POBSP in June 1968 determined the summer population on Islote Negro at 4000 adults and on Islote Afuera at 3000 adults (Crossin MS, 1974). Jehl also found a nearly-grown chick on Gargoyle Rock in April 1970 and Huey (1952) reported a chick there in January 1950. Huey also reported that Hendrickson collected "a number of Oceanodroma petrels from rock crevices on the hillsides of Melpomene Cove, situated on the southern end of Guadalupe Island." We presume that small colonies remain to be discovered on the main island but none are known with certainty. Evidence of the persistence of one or more colonies there is provided by repeated observations of birds landing on ships at the north end of Guadalupe in late spring and summer (Jehl, *pers. obs.*, Anthony 1925, Huey 1930), as well as records of a few petrels flying over the north end of the island in May 1971 (Jehl 1972) and many near the cypress grove in August 1981 (R. Moran, D. Duncan, *pers. comm.*).

The correct nomenclature of the Guadalupe populations has been debated. Van Rossem (1942) pointed out that the type of *socorroensis* was a small bird of the Guadalupe population; since that name had priority, *kaedingi* was relegated to synonymy. When Hubbs (1960) found that two populations were present on Islote Negro, he referred to the summer breeders as *socorroensis* and the winter breeders as *kaedingi.* However, the situation is evidently even more complicated, because the summer birds are highly variable. Crossin (1974) reported that all birds nesting at Islote Negro were dark-rumped, while on Islote Afuera over 90% of the population was white-rumped. Recently, Ainley (1980) named the winter breeders as a new race, *cheimomnestes,* on grounds unconvincing to Bourne and Jehl (1982) but reaffirmed by Power and Ainley (MS).

In summary, Leach's Storm-Petrels breed commonly on islets at the southern end of Guadalupe Island. There is also strong presumptive evidence for the persistence or re-establishment of colonies near the north end and center of the main island. According to Power and Ainley (MS), the winter and summer populations on Islote Negro are temporally segregated and morphologically distinct. If so, their findings would require that the two populations be considered as distinct species, not subspecies. Yet, because of the lack of field work in the fall, neither Bourne and Jehl (1982) nor Crossin (1974: 174) were convinced that the populations are fully isolated temporally. Furthermore, because there are differences in coloration (at least) between summer populations breeding contemporaneously on I. Negro and I. Afuera, and because the morphological characters and breeding seasons are not known for the presumed colonies on the main island, the situation remains unclear. This is one of the most complicated cases of differentiation known in birds, and one that will require additional study.

Ashy Storm-Petrel (*Oceanodroma homochroa*)

A wing attributed to this species by Gaylord (1897) was reidentified as that of *O. leucorhoa* by Anthony (1898*c*). In Gaylord's original report (see above) the presence of an "entirely black" storm-petrel near the colony of *O. macrodactyla* on the main

island was alleged by "hunters." Probably these represented dark-rumped examples of the summer population of *O. l. socorroensis* or, less likely, wanderers of *O. l. chapmani* from the San Benito Islands. *O. homochroa* may occur off Baja California in winter, but the nearest breeding colony is on Los Coronados, 320 km to the north, and may consist of only 2–3 pairs (Jehl *pers. obs.*).

Wedge-rumped Storm-Petrel (*Oceanodroma tethys*)

A specimen obtained in 1950 was said to have been collected from a crevice on the side of Melpomene Cove, at the south end of the main island, which also included a downy young of *O. leucorhoa* (Huey 1952). However, the precise locality is not clear. Howell and Cade (1954) claimed it was collected on Gargoyle Rock at the end of the island, and Hubbs told Jehl the same thing. Jehl landed there in April 1970 and found a single chick of *O. leucorhoa.* There are no subsequent records although the species occurs regularly to southern Baja California (Jehl *pers. obs.*, Pitman *pers. comm.*).

Black Storm-Petrel (*Oceanodroma melania*)

Kaeding (1905) reported this species near Guadalupe, but the observation could have pertained to any of several others. Anthony's (1898*c*) report, which implies that the species nests on Guadalupe Island, actually alludes to the nesting season of the species elsewhere.

Guadalupe Storm-Petrel (*Oceanodroma macrodactyla*)

This endemic and unusual storm-petrel (Fig. 2), originally described as a race of *O. leucorhoa* (Bryant 1887*b*), bred in soil burrows atop the main island, among the pines at the north end and in the cypress grove. Its status and history have most recently been reviewed by Jehl (1972). Both Howell and Cade (1954) and Greenway (1967) incorrectly cite the last report of the species, apparently overlooking the work of Davidson (1928), who corrected earlier errors and established August 1912 as the last acceptable record. A winter breeder, it laid by early March (Kaeding 1905) but sometimes as late as June, for Beck collected three chicks on 3 August 1912 (specimens in AMNH). Nothing is known about the ecology or distribution of this species at sea. Thoburn (1899) reported it as abundant about his ship at night in late June 1897, as it lay anchored at Guadalupe, and reported collecting several. If so, these would represent the only documented records of *macrodactyla* away from the breeding colonies, but we have been unable to locate any specimens and suspect that his reports refer to *O. leucorhoa.*

The Guadalupe Storm-Petrel was considered abundant in the colony as late as 1906 (Thayer and Bangs 1908), but was being preyed upon heavily by domestic cats. Davidson (1928), in declaring it to be extinct, based her conclusion on the negative results of the 1922 expedition by the California Academy of Sciences (Hanna 1925), which took place in mid-summer, after the main breeding season, and on the erroneous assumption that the CAS expedition of April 1925 (McLellan 1926) had carefully searched the breeding grounds. Jehl (1972) spent several nights listening for petrels in the early 1970's in the pine-oak woodlands atop the island, but did not visit the cypress grove, where the species also had nested. No thorough survey of the breeding grounds has been made at the appropriate season since 1906. The apparent persistence of *O. leucorhoa* on the main island despite predation by cats allows some hope that *macrodactyla* may still exist.

As noted above there is no acceptable evidence for the often-repeated contention that Guadalupe and Leach's storm-petrels ever bred in the same colonies. All evidence suggests that they used different habitats: *macrodactyla* burrowed in soil, *leucorhoa* nested in crevices. Further, the breeding season of *macrodactyla* probably overlapped that of the winter and summer forms of *leucorhoa,* so that sequential use of burrows would have been impossible.

Red-billed Tropicbird (*Phaethon aethereus*)

Probably regular in the area but the only records are of individual birds 25 and 37 km north of the island on 11 October 1979, and another slightly farther north on 7 January 1980 (Pitman).

Red-tailed Tropicbird (*Phaethon rubricauda*)

Anthony (1898*b*) reported collecting a specimen close to Guadalupe on 23 July 1897.

Brown Pelican (*Pelecanus occidentalis*)

There are two records, an immature individual reported by Anthony (1925), and a probable juvenile reported on 4 July 1977 (Pierson and Riedman, MS). This coastal species rarely wanders to deep waters beyond the continental shelf.

Double-crested Cormorant (*Phalacrocorax auritus*)

Probably a rare or accidental visitor, but its status requires verification. One was reported by Gaylord (1897) and Huey (1924) casually mentions the species as being present in 1923. Hubbs reported the species on several trips and on 11 June 1955 described a cormorant with "bill and pouch yellow" that would seem to be this species.

Brandt's Cormorant (*Phalacrocorax penicillatus*)

Resident. Seen regularly in small numbers along the entire east side of the island but commonest near the southern end, where a few pairs breed on outer islet (McLellan 1926, Crossin MS), and on Islote Zapato (Hubbs notes, Jehl *pers. obs.*). The maximum single count is 20 at I. Zapato on 4 May 1966. We suspect that the entire island population does not exceed 30–40 individuals. Specimens in SDNHM.

Pelagic Cormorant (*Phalacrocorax pelagicus*)

J. Sefton reported this species on Hubbs' expedition of 27 January–3 February 1950 (Hubbs field notes). His identifications were doubted by Hubbs, and by us.

Magnificent Frigatebird (*Fregata magnificens*)

Sightings of an immature on 1 and 4 July 1973 (Pierson and Riedman, MS) probably represent the same individual.

Great Blue Heron (*Ardea herodias*)

Probably a rare but regular winter visitor. Hubbs saw one or more on five different trips (maximum three, two trips), between November and February. Other records are: 1, September 1896 (Gaylord 1897); 2–3 in summer 1922 (Anthony 1925); and 1, midwinter 1965 (Kenyon MS).

White-fronted Goose (*Anser albifrons*)

Bryant (1887*a*) shot one on 14 January 1885, but it fell over a cliff and could not be recovered.

Brant (*Branta nigricans*)

Mirsky (MS) reported a sick bird at Northeast Anchorage on 22–24 November 1973.

Mallard (*Anas platyrhynchos*)

Hubbs saw several and collected single males on 13 and 17 December 1957 (LACMNH).

Northern Pintail (*Anas acuta*)

Pitman saw one 40 km north of the island on 11 October 1979.

Blue-winged Teal (*Anas discors*)

Hubbs reported collecting an adult male on 30 October 1957. The location of the specimen, if preserved, is unknown.

Cinnamon Teal (*Anas cyanoptera*)

Jehl saw a male swimming along the shore of the main island on 21 January 1970.

Lesser Scaup (*Aythya affinis*)

Hubbs' field notes list "a female or immature male" several kilometers from the island on 22 November 1964.

Red-breasted Merganser (*Mergus serrator*)

This species probably is an occasional winter visitor. There are two records: 28 January 1950 (Hubbs), and 13–17 December 1973 (Mirsky MS).

Osprey (*Pandion haliaetus*)

Status uncertain. Ospreys have nested on many islands along the Baja California peninsula and perhaps formerly bred on Guadalupe, although proof is lacking. Specimens were collected 11 July 1922 (Anthony 1925, Hanna 1925) and on 25 July 1941 (Bond and Meyer de Schauensee 1944). Kenyon (MS) visited Guadalupe early in 1965 and saw no Ospreys but reported two presumed nests near the north end of the island. There are no other reports or indications of the species' presence.

Red-tailed Hawk (*Buteo jamaicensis*)

Formerly resident in small numbers. Howell and Cade (1954) considered it "apparently resident until at least 1932," but none of the early explorers were able to find any nests. Palmer (*in* Bryant 1887*a*) considered it as common as the caracara. Thayer and Bangs (1908) and Anthony (1925) reported that three or four could be seen in a day; Hanna (1925) also considered it common. This hawk wanders to many offshore islands in fall migration and probably reaches Guadalupe infrequently. However, we know of no recent reports for any season, and it is not resident at this time.

Crested Caracara (*Polyborus plancus lutosus*)

Extinct; formerly resident in small numbers. The detailed history of this endemic form and its taxonomy have been reviewed by Abbott (1933) and Brown and Amadon (1968).

American Kestrel (*Falco sparverius*)

Resident in small numbers. Bryant (1887*a*) stated that they were found most often in the central and higher portions of the islands. Howell and Cade (1954) reported a pair with young on a cliff overlooking the sea at Northeast Anchorage; other birds were in the area. In recent years the species has been seen regularly near Northeast Anchorage and at the southern end of the island. D. A. Duncan (*pers. comm.*) visited Guadalupe 19–26 August 1981 and reported it as common everywhere, one or two being seen at

most localities. The Guadalupe population was described as an endemic race (*guadalupensis*) by Bond (1943); its validity was accepted by the AOU Check-list (1957) though not by the Mexican Check-list (Friedmann, Griscom, and Moore 1950).

Peregrine Falcon (*Falco peregrinus*)

This large, maritime falcon is likely to have occurred regularly during migration, but we know of only one report, a single bird seen on 19 September 1896 (Gaylord 1897).

Prairie Falcon (*Falco mexicanus*)

Bryant (1889) reported that the species was seen on "two or three occasions" in 1886, but we suspect that these sightings pertain to the Peregrine Falcon.

Pacific Golden Plover (*Pluvialis fulva*)

Jehl saw a flock of 20, two km north of the settlement at the south end on 22 February 1969. Mirsky (MS) reported from 1 to 12 birds along the shore at Northeast Anchorage from 23 November–16 December 1973. Presumably all records of golden plovers pertain to this species (*see* Connors 1983).

Killdeer (*Charadrius vociferus*)

Hubbs reported two on 13 December 1957.

Willet (*Catoptrophorus semipalmatus*)

The only report is a single bird observed between 10–14 February 1977 (E. Chu).

Wandering Tattler (*Heteroscelus incanus*)

This is a regular visitor to the island from fall through spring; there is one summer record. One or two, often more, are seen on most trips.

Ruddy Turnstone (*Arenaria interpres*)

Though not reported by Howell and Cade (1954), this species is a regular visitor in small numbers. There are specific records for June, November–January, and April. At least three were present in November 1964 (Hubbs). Hubbs also collected several specimens, the location of which is not known.

Black Turnstone (*Arenaria melanocephala*)

Uncommon but regular in migration and during the winter. There are records for October–February, and April. The maximum count is seven on 20–26 January 1970 (Hubbs, Jehl). Specimen LACMNH.

Sanderling (*Calidris alba*)

Two were seen on 22 January 1970 (Jehl).

Western Sandpiper (*Calidris mauri*)

One was photographed at Northeast Anchorage on 16 April 1978 (Everett).

Short-billed Dowitcher (*Limnodromus griseus*)

Hubbs collected an immature that landed on his boat about 2 km off the south end of the island on 29 August 1956 (LACMNH).

Common Snipe (*Gallinago gallinago*)

One record, atop the northern end of the island on 8 June 1953 (Howell and Cade 1954).

Red Phalarope (*Phalaropus fulicaria*)

Regular in migration. This phalarope is seen irregularly, sometimes in fair numbers, between November and May; it has also been reported in late June (Thayer and Bangs 1908).

Jaegers (*Stercorarius* spp.)

Jaegers certainly occur near the island during migration, but the only published record seems to be that of Gaylord (1897), who reported two Long-tailed Jaegers (*S. longicaudus*) on 17 September 1896. Pitman has seen several jaegers in the area in January, and identified a Pomarine (*S. pomarinus*) on 4 January 1980.

Heermann's Gull (*Larus heermanni*)

Two adults were photographed by S. Leatherwood in January 1973 (photo HSWRI).

Ring-billed Gull (*Larus delawarensis*)

Jehl and R. DeLong saw one immature at Northeast Anchorage on 22 January 1970. This species rarely ventures beyond the coastal beaches. Hubbs reported "a few" on 28 January 1950, but his identification seems questionable.

California Gull (*Larus californicus*)

Though not recorded by Howell and Cade (1954), this gull is a regular, sometimes common, winter visitor. It avoids the elephant seal beaches, because of competition with the larger gulls, and tends to occur at sea. Twenty in February 1978 (Chu et al. MS) is the largest number recorded (but *see* Herring Gull).

Herring Gull (*Larus argentatus*)

Common winter visitor from November–April, at times being as common as the Western Gull. Hubbs reported that it was by far the commonest gull in January–February 1950, and counted 360 at the south end of the island in late January 1960. However, we suspect that many of these were California Gulls, for at that season Herring Gulls congregate near the elephant seal rookeries.

Thayer's Gull (*Larus thayeri*)

Uncommon but regular winter visitor. There are several records, all for immature or sub-adult birds; 21 February 1969, 16 April 1970, 30 January 1971 (3) and 15 March 1971 (Devillers et al. 1971).

Western Gull (*Larus occidentalis*)

This species is resident at Guadalupe. Hubbs recognized that the local population differed slightly from the mainland birds. There are minor differences in the color of the fleshy parts (Howell and Cade 1954) and also in the pattern of the primary markings. Hubbs (1960) suggested that it might represent an endemic race, but no formal analysis of the variation has been attempted. In winter the local population is probably enhanced by representatives from the mainland, as both Hubbs and Jehl have seen many birds with pinkish (rather than whitish) legs at that season.

In Jehl's opinion the population in 1969–71 consisted of only 30–40 pairs. Crossin (MS) reported that the species is "rather sparse," and guessed that the local population

in June was no larger than 200 birds. Jehl found a nest with three eggs near the old Lobster Camp on 21 May 1971, and Crossin reported another on Islote Afuera on 20–23 June 1968. In contrast to mainland gulls, the Guadalupe birds nest singly, well back from the shore, and there is no evidence of colonies. In November–December 1973, Mirsky reported 100 at the Northeast Anchorage; all had whitish legs. Chu et al. (MS) counted 100–125 along the entire eastern shore of the island in February 1978, and noted that adults outnumbered juveniles by about 10:1. Pierson and Riedman (MS) reported at least 100 birds during a circumnavigation in the first week of July 1977, most of which were attending nests; at least 15 large nestlings were seen.

Bryant (1887*a*) was told that gulls nested commonly at the southern end of the island, "where they were not so frequently molested by the 'Quelelis'" (=Caracaras).

Glaucous-winged Gull (*Larus glaucescens*)

Regular winter visitor, most frequently reported at the Northeast Anchorage in January–March, when they and other gulls feed on elephant seal remains and placentas. Up to 25, adults and immatures, have been seen at that time (Kenyon, MS). There are records from November–May, the latest being 1 May 1967 (Hubbs).

Black-legged Kittiwake (*Rissa tridactyla*)

The Kittiwake occurs in winter; it is common in some years, absent in others. Flocks of up to 100 were seen around the island on 20–26 January 1970 by Hubbs and Jehl.

Sabine's Gull (*Xema sabini*)

This migrant is probably uncommon but regular in spring and fall. Hubbs reported 10 birds 5 km east of the island on 26 April 1967. An additional report, on 27 January 1950 (Hubbs) almost certainly pertains to an immature kittiwake.

Royal Tern (*Sterna maxima*)

Gaylord (1897) reported one near the island on 17 September 1886.

Arctic Tern (*Sterna paradisaea*)

This species certainly occurs regularly off the coast of Baja California, but there are few records. Pitman identified one near the island on 11 October 1979 and saw a second tern, probably of the same species.

Xantus Murrelet (*Synthliboramphus hypoleuca*)

This small alcid breeds on at least two of the small islets at the southern end of the main island; the nesting grounds were discovered by Hubbs. Crossin (MS) estimated the Islote Negro population at 800 birds (300 non-breeding) and the Islote Afuera population at 4000 birds (1000 non-breeding) in June 1968. In 1977 remains of nine birds were found in caves along cliffs at the east side of the island (Pierson and Riedman MS), which suggests the possibility of a mainland breeding locale.

The species occurs near the islands from late December through August, and many fly aboard ships at night. The birds apparently first visit the nesting grounds in February. Hubbs found none on the islands between October and January (five trips total) but found fresh eggs as early as 5 March. The peak of the breeding season is late April–June. Yet, the breeding season may be protracted, as Hubbs found fresh eggs as late as 29–30 August. Brownell (MS) reported that "adequate nesting grounds on the small islotes off Guadalupe are almost fully utilized." If so, nest site limitation would be a strong selective agent for an expanded breeding season, as has apparently occurred in Leach's Storm-Petrels.

Geographic variation in the species has been discussed by Jehl and Bond (1975); the local form is *S. h. hypoleuca.*

Cassin's Auklet (*Ptychoramphus aleuticus*)

Although many ornithologists have noted this species at Guadalupe, particularly near the southern end of the island (e.g., Thayer and Bangs 1908), it remained for Hubbs to discover the nesting area on Islote Negro. The species is not known to nest on Islote Afuera (Crossin MS). Brownell (MS) estimated the population at 200 pairs in April 1968, a figure that is supported by Hubbs' and Jehl's data.

Hubbs and associates banded many birds on I. Negro. In 1968 Brownell banded 56 and recovered two that had been banded two years earlier, one as an adult and one as a downy chick. Other banded birds were recovered in April 1970 (Jehl *pers. obs.*), but details are not available.

The breeding season begins in January. Hubbs reported nests with fresh eggs on 30 January. The peak in laying occurs by April and by late April many nests may contain young. There is annual variation in the nesting period. For example, on 19 April 1957 Hubbs reported numerous burrows, fresh eggs, eggs with embryos, newly hatched young, and well-developed young; on 23 April 1963, 27 nests contained only downy young. In most years nesting is completed by late June. On 13 June 1955 Hubbs found young ready to fledge. On 22 June 1968, most of the colony had completed nesting; 85 adults and 40 chicks were present (Crossin MS).

Rhinoceros Auklet (*Cerorhinca monocerata*)

Probably an irregular winter visitor. There are records for 19 April 1925 (McLellan 1926), 9 February 1957 (Hubbs, specimen LACMNH), and 4 January 1980 (Pitman).

Rock Dove (*Columba livia*)

According to Hubbs, the species was introduced to the island in 1956 by residents of the settlement. Kenyon (MS) reported 20 at the weather station in 1965. In 1977 flocks of up to six were recorded at Twin Canyons and the Lobster Camp (Pierson and Riedman MS). Six were seen in the village (along with a peafowl [*Pavo cristatus*]), on 5 May 1980 (Everett), and Duncan reported 15–20 there on 19–26 August 1981.

White-winged Dove (*Zenaida asiatica*)

A specimen of *Z. a. mearnsi* was collected on 10 June 1953 (Howell and Cade 1954).

Mourning Dove (*Zenaida macroura*)

This species was considered accidental by Howell and Cade (1954), perhaps based on the report of Gaylord (1897). It has since colonized the island. Hubbs made the following observations: 31 August 1956—1; 23 November 1964—1; 10–14 February 1967—24 near the Lobster Camp. By 1970 the species was widespread. Jehl found a nest with two young near the village on 14 April and found a pair, almost certainly with a nest, at the Lobster Camp on 16 April. Another pair was present on Islote Negro on 18 April. In November–December 1973, Mirsky (MS) reported a few at Northeast Anchorage and 30 or more near springs. In August 1981, D. Duncan (*pers. comm.*) estimated the population to be in the low hundreds.

Great Horned Owl (*Bubo virginianus*)

The presence of large owls has not been verified. Bryant (1887*a*) reported that "Dr. Palmer's assistant" stated that a large owl (*Bubo*) was present on the island, and further noted that the Mexican inhabitants reported hearing "hooting" at night. They said, however, that the owl was very rare. Ridgway (1876) also noted that "two kinds of

owls were seen" by the Palmer party but that no specimens were taken. In 1981, the base commander told D. Duncan of large owls in the canyons to the south of the airstrip.

Burrowing Owl (*Athene cunicularia*)

This small owl is widespread and common on the main island; it also occurs on Islote Negro. The island population is indistinguishable from the mainland form (*A. c. hypugaea*) (Thayer and Bangs 1908).

Vaux's Swift (*Chaetura vauxi*)

One was seen at the Sealer's Camp on 5 May 1980 (Everett).

White-throated Swift (*Aeronautes saxatalis*)

"Regular visitor, at least formerly. Unreported since 1922" (Howell and Cade 1954).

Anna's Hummingbird (*Calypte anna*)

According to Howell and Cade (1954) this hummingbird was evidently uncommon to rare prior to 1953 but shortly thereafter became established in the *Nicotiana* grove at Northeast Anchorage. However, Bryant (1887*a*) was told that they were common in palms on the northwestern slope and collected one. Howell and Cade (1954) estimated the population at 15–20 birds and called attention to the different song of the local population, a difference subsequently established by Mirsky (1976). Mirsky estimated the population at approximately 100 individuals. On 19 May 1971, Jehl found a nest with two eggs in a low shrub near the top of the island, in a canyon above Barracks Beach.

Allen's Hummingbird (*Selasphorus sasin*)

Power (1972) incorrectly listed this species as breeding. We know of no evidence for its occurrence.

Belted Kingfisher (*Ceryle alcyon*)

Although not listed by Howell and Cade (1954), the kingfisher is an uncommon but regular winter visitor. Between 1957–1969, Hubbs had eight records (nine individuals) between 25 October and 20 April. It has since been reported almost annually (many observers).

Northern Flicker (*Colaptes auratus rufipileus*)

This endemic race was formerly resident in the forested areas atop the island but is now probably extinct. Habitat depletion and predation by cats have been considered the responsible agents. Apparently it was fairly common and as late as 1906, when last seen, the population was reported as "not more than forty individuals" (Thayer and Bangs 1908). The history of this local population has been reviewed by Greenway (1967); see also Grinnell (1928).

There are recent reports of flickers at Guadalupe. K. Briggs (*pers. comm.*) reported the species in the pine forest on 17–18 December 1972, and Mirsky (MS) saw one at Northeast Anchorage in late November–early December 1973; whether these are fall migrants from the mainland or remnants of the endemic population is unresolved.

Least Flycatcher (*Empidonax minimus*)

Accidental. A specimen of this eastern species was taken on 25 October 1962 (Stager, specimen LACMNH).

Say's Phoebe (*Sayornis saya*)

The only report is of eight at Northeast Anchorage in November–December 1973 (Mirsky MS).

Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)

Single birds were seen on 23 November 1964 (Hubbs) and on 18 May 1971 (Jehl).

Barn Swallow (*Hirundo rustica*)

Two seen on 19 May 1971 (Jehl) were presumed to be migrants.

Clark's Nutcracker (*Nucifraga columbiana*)

In the invasion year of 1972, at least one nutcracker was observed in the pine forest at the north end of the island on 17–18 December (K. Briggs *pers. comm.*).

Red-breasted Nuthatch (*Sitta canadensis*)

This nuthatch is resident in small numbers in the pine woods at the north end of the island. In 1971 Jehl found five pairs there, and on 12–13 April 1970 he observed two pairs feeding young and found an additional nest. It occurred in the cypress grove in 1953 (Howell and Cade 1954) and probably still does.

Rock Wren (*Salpinctes obsoletus guadalupensis*)

This endemic race is abundant in all open areas of the island, from the beach to the crest; it is much less common in forested areas. In 1981, in one open area on top of the island, D. Duncan counted one wren per 50 m in a 20 m wide transect. There are no current estimates of numbers, but the total population is certainly in the thousands.

Bewick's Wren (*Thryomanes bewickii brevicauda*)

Extinct, last seen in 1892 (Anthony 1901). The history of this endemic form has been reviewed by Grinnell (1928) and Greenway (1967). It resided in brushy areas and pines, but was never numerous. Habitat depletion by goats and predation by cats caused its demise.

Ruby-crowned Kinglet (*Regulus calendula obscurus*)

This endemic race formerly nested in the cypress grove as well as in the pine forest, and apparently was fairly common. Howell and Cade (1954) reported five singing males in the cypress grove on 11 June 1953. Mirsky (MS) reported five in the cypress grove, two in the pine-oak grove, and one in the *Nicotiana* (presumably near the beach) in November–December 1973. However, birds seen in winter could be migrants and the current status of the endemic population requires verification.

Mountain Bluebird (*Sialia currucoides*)

Three wintered on Guadalupe in 1885–86; one was collected (Bryant 1887*a*).

Townsend's Solitaire (*Myadestes townsendi*)

One seen on 22 March 1897 (Kaeding 1905) is the only record.

Hermit Thrush (*Catharus guttatus*)

Bryant (1887*a*) collected three in the cypress woods between December 1885 and March 1886. The race has not been verified (Miller et al. 1957).

American Robin (*Turdus migratorius*)

Bryant (1887*a*) saw several in December–January 1886–87 in the cypress grove. Mirksy (MS) saw one at Northeast Anchorage on 5 December 1973.

Varied Thrush (*Ixoreus naevius*)

One was observed in the pine forest on 4 March 1886 (Bryant 1887*a*).

Northern Mockingbird (*Mimus polyglottos*)

Considered accidental by Howell and Cade (1954), apparently on the basis of a report by Bryant (1887*a*), who saw two and collected one on 16 March 1886. One was described to Jehl on 22 February 1969.

Sage Thrasher (*Oreoscoptes montanus*)

One was collected on 7 January 1886 (Bryant 1887*a*).

Water Pipit (*Anthus spinoletta*)

This pipit is probably rare but regular in migration. Bryant reported a flock of 25 on 2 February 1886 (Bryant 1887*a*).

Cedar Waxwing (*Bombycilla cedrorum*)

Bryant (1887*a*) collected one in the winter of 1885–86.

Loggerhead Shrike (*Lanius ludovicianus*)

Bryant (1887*a*) saw two and collected a female that had fed on a Ruby-crowned Kinglet on 29 December 1885. The other bird was heard singing, which suggests the possibility of a mated pair.

European Starling (*Sturnus vulgaris*)

On 15 May 1971, Jehl saw one at the settlement at the south end of the island, and on 18 May found three in the pine forest at the north end of the island.

Yellow-rumped (Audubon's) **Warbler** (*Dendroica coronata*)

This warbler is probably a regular winter visitor. It was first reported by Bryant (1887*a*) and has been seen by many observers. Mirsky (MS) reported up to 30 in November–December 1973 at Northeast Anchorage. Everett saw an example of the eastern race (*D. c. coronata*) on 18 April 1979.

Townsend's Warbler (*Dendroica townsendi*)

Mirsky (MS) reported three in the pine-oak woods on 6 December 1975.

Black-and-white Warbler (*Mniotilta varia*)

One in the pine forest, 19 May 1971 (Jehl).

Ovenbird (*Seiurus aurocapillus*)

A specimen of *S. a. aurocapillus* was collected on 9 June 1953 (Howell and Cade 1954). The late date is typical for eastern vagrants on the west coast in spring.

Common Yellowthroat (*Geothlypis trichas*)

One was collected on 12 November 1938 (Huey 1954).

Wilson's Warbler (*Wilsonia pusilla*)

Probably regular in migration but there are only two records; 18 May 1971 (Jehl) and 18 April 1979 (Everett).

Summer Tanager (*Piranga rubra*)

A specimen of the eastern race (*P. r. rubra*) was collected in the cypress grove on 12 October 1913 (Kimball 1922).

Rose-breasted Grosbeak (*Pheucticus ludovicanus*)

Two records, 24 October 1962 (Stager, specimen LACMNH) and 5 December 1973 (Mirsky, specimen UCLA).

Black-headed Grosbeak (*Pheucticus melanocephalus*)

The wing of a male was found on the east side of the island on 29 June 1977 (Pierson and Riedman MS).

Guadalupe Rufous-sided Towhee (*Pipilo erythrophthalmus consobrinus*)

Extinct. The history of this endemic race has been summarized by Grinnell (1928) and more fully by Greenway (1967). It was known to occur in the cypress grove and perhaps elsewhere, and was last observed in 1897. Its extinction was due to habitat depletion by goats and predation by cats.

Chipping Sparrow (*Spizella passerina*)

Bryant (1887*a*) collected one on 6 January 1886, and Mirsky (MS) reported the species in the *Nicotiana* and in the pine-oak forest in November–December 1973.

Fox Sparrow (*Passerella iliaca*)

An example of *P. i. sinuousa* collected on 16 February 1886 (Bryant 1887*a*), seems to represent the southernmost record for the species on the Pacific coast.

Lincoln's Sparrow (*Melospiza lincolnii*)

Bryant (1887*a*) collected individuals on 5 and 19 February 1886, and Swarth (1933) reported a specimen taken on 16 March 1932.

White-throated Sparrow (*Zonotrichia albicollis*)

One collected, 10 October 1913 (Kimball 1922).

Golden-crowned Sparrow (*Zonotrichia atricapilla*)

Bryant (1887*a*) collected two on 16 February and one on 4 March 1886, in the pines.

White-crowned Sparrow (*Zonotrichia leucophrys*)

Probably regular in migration but the only report is of two near the south end of the island on 14 April 1970 (Jehl).

Guadalupe Dark-eyed Junco (*Junco hyemalis insularis*)

Knowledge of this endemic junco was fully summarized by Howell (1968); additional information, including variation in the song, was provided by Mirsky (1976). At one time the junco was one of the most abundant birds on the island (Palmer, in Ridgway 1876). Today it is uncommon and is much less abundant than the House

Finch or Rock Wren. It may be found scattered along the northern half of the island wherever there is vegetation. It often feeds on the ground, in litter at the base of pine trees but also in the oaks. However, it seems adaptable and now occupies stands of *Nicotiana* on the beach. Breeding occurs from late January (Bryant 1887*a*) to at least late April (Howell 1968). On 17 May 1971 Jehl saw young juncos that were independent of the parents. The taxonomic relationships of this junco have been fully discussed by Miller (1941), who argued that the local population was derived from migratory ancestors. "The Guadalupe junco is distinguished principally by its relatively long bill and short wing and tail . . . and virtual absence of sexual dimorphism in color" (Howell 1968). The long bill is used to extract seeds from deep in pine cones (Jehl *pers. obs.*). Power (1980) also discussed the morphology of this species. Bryant (1887*a*) collected a migrant of one of the mainland races (*thurberi*?, cf. Miller et al. 1957) on 6 January 1886, that was being attacked by a resident junco.

Western Meadowlark (*Sturnella neglecta*)

Bryant (1887*a*) reported one on the crest of the island on 22 March 1886.

Brewer's Blackbird (*Euphagus cyanocephalus*)

A female was seen on 12 December 1973 (Mirsky MS).

Scott's Oriole (*Icterus parisorum*)

Mirsky (MS) reported two males and three females in the *Nicotiana* at Northeast Anchorage from 23 November to 3 December 1973.

Guadalupe House Finch (*Carpodacus mexicanus amplus*)

This endemic, the second commonest landbird, may occur almost anywhere, including Islote Negro, but is most common near vegetation and at the village. The entire population may exceed 1000. Bryant (1887*a*) provided information on nests and nest sites. He also noted that the finches were captured and eaten by locals. The evolution and geographic variation of this race have been reviewed by Power (1979).

Red Crossbill (*Loxia curvirostra*)

Howell and Cade (1954) reported this species as "formerly resident; no definite breeding record; unreported since 1903." Evidently it was once fairly common as Bryant (1887*a*) reported about 20 in the pines in 1886, and reported collecting nine specimens, including an immature in February–March 1896. According to K. C. Parkes, six birds collected by A. W. Anthony on 20 September 1896 include a female almost molted out of juvenile plumage and five full-grown juveniles. The species was also reported as being "resident" by Gaylord (1897), though he did not observe it. Kaeding (1905) reported "a few" in 1897. Grinnell (1928) reviewed the status of the species and examined the specimens, which he attributed to *L. c. bendirei*. A. R. Phillips, however, now refers all specimens to *L. c. benti* (*fide* K. C. Parkes).

Goldfinch (*Carduelis* sp.)

Townsend (1916) states "the Goldfinch was observed." There is no additional information.

Discussion

The Guadalupe avifauna was well-studied in the late 19th and early 20th centuries. Recent studies have provided new information on seabirds; yet, much remains to be learned. The known colonies are difficult to reach and most visits to them have been made in winter or spring. Studies during other seasons are needed to clarify breeding

seasons. Efforts are also needed to locate seabird colonies on the main island, especially in light of recent reports of storm-petrels calling there at night, and to determine the morphological characters of any such populations. It is not inconceivable that the Guadalupe Storm-Petrel has escaped extinction.

The island's rugged topography and lack of fresh water have inhibited recent work along the central axis. Surveys in forested areas during the breeding season are needed to determine the status of the endemic races of the Ruby-crowned Kinglet and Northern Flicker. Both species are common on the mainland and highly migratory, so sight records are not proof of the persistence of endemic races. Even evidence of breeding may be equivocal, as secondary invasions by these species could have taken place. These studies will be difficult and will require capturing or collecting some birds.

Faunas of oceanic islands are not constant. New species arrive regularly; some become established, and others disappear. The factors that affect successful colonization or promote extinction are difficult to establish (Jehl and Parkes 1983) but are critical to understanding avian distribution. On Guadalupe, a new food source (*Nicotiana glauca*), may have been a major factor in allowing Anna's Hummingbirds to colonize (or become more common?) in the past several decades. Mourning Doves have also become established, though the reasons why are unstudied.

In view of the importance of island faunas to current theories in biogeography, regular surveys should be encouraged (e.g., at least every decade) so that changes can be detected as they are occurring or shortly afterward. Such data will be especially useful from islands, like Guadalupe, where a strong historical record has been established.

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Literature Cited

Abbott, C. G. 1933. Closing history of the Guadalupe Caracara. Condor 35:10–14.

Ainley, D. G. 1980. Geographic variation in Leach's Storm-Petrel. Auk 97:837–853.

———. 1983. Further notes on variation in Leach's Storm-Petrel. Auk 100:230–233.

American Ornithologists' Union. 1957. Check-list of North American Birds. Fifth Edition. Lord Baltimore Press, Baltimore, Maryland.

———. 1983. Check-list of North American Birds. Sixth Edition. Allen Press, Lawrence, Kansas.

Anon. 1874. Guadalupe. La isla de la piel de oro, sin duda alguna. Forest and Stream 2(22):337–338.

Anthony, A. W. 1898*a*. Two new birds from the Pacific coast of America. Auk 15:36–38.

———. 1898*b*. Four sea birds new to the fauna of North America. Auk 15:38–39.

———. 1898*c*. Petrels of Southern California. Auk 15:140–144.

———. 1900. Nesting habits of the Pacific Coast species of the genus *Puffinus*. Auk 17:247–252.

———. 1901. The Guadalupe Wren. Condor 3:73.

———. 1925. Expedition to Guadalupe Island, Mexico, in 1922. The birds and mammals. Proceedings California Academy Sciences, Series 4 14:277–320.

Austin, O. L., Jr. 1952. Notes on some petrels of the North Pacific. Bulletin Museum Comparative Zoology. 107:391–403.

Bent, A. C. 1922. Life histories of North American petrels and pelicans and their allies. United States National Museum Bulletin 121.

Blake, S. F. 1961. Edward Palmer's visit to Guadalupe Island, Mexico, in 1875. Madrono 16: 1–4.

Bond, J., and R. Meyer de Schauensee. 1944. Fifth George Vanderbilt Expedition (1941). Academy Natural Sciences Philadelphia Monograph 6.

Bond, R. M. 1943. Variation in western sparrow hawks. Condor 45:168–185.

Bourne, W. R. P., and J. R. Jehl, Jr. 1982. Vari-

ation and nomenclature of Leach's Storm-Petrel. Auk 99:793–797.

Brown, L., and D. Amadon. 1968. Eagles, Hawks and Falcons of the World. 2 vols. McGraw-Hill, New York.

Brownell, R. L., Jr. MS. Preliminary report eastern area cruise number 40, Isla Guadalupe [1968]. Smithsonian Institution, Pacific Ocean Biological Survey Program. 8 pp.

Bryant, W. E. 1887*a*. Additions to the ornithology of Guadalupe Island. Bulletin California Academy Sciences Series 2 2:269–318.

———. 1887*b*. Description of a new subspecies of petrel from Guadalupe Island. Bulletin California Academy Sciences, Series 2 2:450–451.

———. 1889. A catalogue of the birds of lower California, Mexico. Proceedings California Academy Sciences, Series 2 2:237–320.

Chu, E. W., B. Tyler and D. Lewis. MS. Avian notes. pp. 12–31 *in* M. Pierson (ed.). Report of a Scripps Institution of Oceanography Expedition to Baja California Islands, 9–20 Feb. 1978.

Connors, P. G. 1983. Taxonomy, distribution, and evolution of Golden Plovers *Pluvialis dominica* and *Pluvialis fulva*. Auk 100:607–620.

Crossin, R. S. MS. Preliminary report of Guadalupe Island [1968]. Smithsonian Institution, Pacific Ocean Biological Survey Program. 8 pp.

———. 1974. The storm-petrels (*Hydrobatidae*). pp. 154–205 *in* W. B. King (ed.). Pelagic studies of seabirds in the Central and Eastern Pacific Ocean. Smithsonian Contributions Zoology 158.

Davidson, M. E. McLellan. 1928. On the present status of the Guadalupe petrel. Condor 30:355–356.

DeLong, R. L. and R. S. Crossin. MS. Status of seabirds on Islas de Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados.

Devillers, P., G. McCaskie, and J. R. Jehl, Jr. 1971. The distribution of certain large gulls (*Larus*) in southern California and Baja California. California Birds 2:11–26.

duPetit-Thouars, A. 1956. Voyage of the *Venus* Sojourn in California. Excerpt from "Voyage autour du monde sur la fregate *Venus* pendant les annees 1836–1839. Translated by C. N. Rudkin. Los Angeles, Glen Dawson Press.

Emerson, W. O. 1906. *Oceanodroma leucorhoa* and its relatives on the Pacific coast. Condor 8:53–55.

Friedmann, H., L. Griscom, and R. Moore. 1950. Distributional check-list of the birds of Mexico. Pacific Coast Avifauna 29.

Gaylord, H. A. 1897. Notes from Guadalupe Island. Nidologist 4:41–43.

Godman, F. D. 1907–1910. A monograph of the petrels. Witherby, London.

Greenway, J. C. 1967. Extinct and Vanishing Birds of the New World. Dover Publications. New York.

Grinnell, J. 1918. The status of the white-rumped petrels of the California coast. Condor 20:46.

———. 1928. A distributional summation of the ornithology of Lower California. University California Publications Zoology 32(1):1–300.

Hanna, G Dallas. 1925. Expedition to Guadalupe Island, Mexico, in 1922. General Report. Proceedings California Academy Sciences Series 4 14:217–275.

Howell, T. R. 1968. Guadalupe Junco. pp. 1094–1098 *in* A. C. Bent et al. (O. L. Austin, Jr. [ed.]). Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. United States National Museum Bulletin 237.

———, and T. J. Cade. 1954. The birds of Guadalupe Island in 1953. Condor 56:283–294.

———, and ———. 1955. Additional data on the birds of Guadalupe Island. Condor 58:78.

Hubbs, C. L. 1960. The marine vertebrates of the outer coast. Systematic Zoology 9:134–147.

———, and J. R. Jehl, Jr. 1976. Remains of Pleistocene birds from Isla de Guadalupe, Mexico. Condor 78:421–422.

Huey, L. M. 1924. A trip to Guadalupe, the isle of my boyhood dreams. Natural History 24: 578–588.

———. 1925. Guadalupe Island: an object lesson in man-caused devastation. Science 61:405–407.

———. 1930. Notes on the habits and plumage of young Kaeding Petrels. Condor 32:68–69.

———. 1952. *Oceanodroma tethys tethys*, a petrel new to the North American avifauna. Auk 69: 460–461.

———. 1954. Notes from Southern California and Baja California, Mexico. Condor 56:51–52.

Jehl, J. R., Jr. 1972. On the cold trail of an extinct petrel. Pacific Discovery 25(6):24–29.

———, and S. I. Bond. 1975. Morphological variation and species limits in murrelets of the genus *Endomychura*. Transactions San Diego Society Natural History 18:9–23.

———, and K. C. Parkes. 1983. "Replacements" of landbird species on Socorro Island, Mexico. Auk 100:551–559.

Johnson, C. W. 1953. Notes on the geology of Guadalupe Island, Mexico. American Journal Science 251:231–236.

Kaeding, H. B. 1905. Birds from the west coast of Lower California and adjacent islands. Condor 7:105–138.

Kenyon, K. W. MS. Expedition to Baja California, Mexico 19 Jan.–11 Feb. 1965. Unpublished report to U.S. Fish and Wildlife Service.

Kimball, H. H. 1922. Bird records from California, Arizona, and Guadalupe Island. Condor 24:96–97.

Lewis, L. R. 1971. Baja Sea Guide, Vol. 2. Miller Freeman Publications, San Francisco.

Lindsay, G. 1966. Guadalupe Island. Pacific Discovery 19:2–11.

Loomis, L. M. 1918. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. 12. A review of the albatrosses, petrels, and diving petrels. Proceedings California Academy Sciences Series 4 2:1–187.

Madden, H. M. 1949. Xantus, Hungarian naturalist in the pioneer west. Palo Alto, California. Books of the West.

McLellan, M. E. 1926. Expedition to the Revillagigedo Islands, Mexico, in 1925. VI. The birds

and mammals. Proceedings California Academy Sciences Series 4 15:279–322.
Miller, A. H. 1941. Speciation in the avian genus *Junco*. University California Publications Zoology 44:173–434.
Miller, A. H., H. Friedmann, L. Griscom, and R. T. Moore. 1957. Distributional check-list of the birds of Mexico. Pacific Coast Avifauna No. 33.
Mirsky, E. N. MS. The Guadalupe Island avifauna in 1973.
———. 1976. Song divergence in hummingbird and junco populations on Guadalupe Island. Condor 78:230–235.
Oberholser, H. C. 1917. A review of the subspecies of the Leach Petrel, *Oceanodroma leucorhoa* (Vieillot). Proceedings United States National Museum 54:165–172.
Palmer, R. S. (ed.). 1962. Handbook of North American Birds. Vol. 1. Yale University Press, New Haven and London.
Pierson, M., and M. Riedman MS. Report of an expedition to Isla de Guadalupe, Baja California, Mexico 20 June–13 July 1977. Unpublished Report, Univ. Calif. Santa Cruz. 15 pp.
Power, D. M. 1972. Numbers of bird species on the California Islands. Evolution 26:451–463.
———. 1979. Evolution in peripheral isolated populations: *Carpodacus* finches on the California Islands. Evolution 33:834–847.
———. 1980. Evolution of land birds on the California Islands. pp. 613–650 *in* D. M. Power (ed.). The California Islands: Proceedings of a multidisciplinary symposium. Santa Barbara Museum Natural History.
———, and D. G. Ainley. MS. Similarity among populations of Leach's Storm-Petrels.
Ridgway, R. 1876. Ornithology of Guadeloupe [sic] Island, based on notes and collections made by Dr. Edward Palmer. United States Geological and Geographical Survey Territories 2:183–195.
Rothschild, W., and E. Hartert. 1902. Further notes on the fauna of the Galapagos Islands. Notes on birds. Novitates Zoologica 9:381–418.
Small, A. 1961. Southern Pacific Coast Region. Audubon Field Notes. 15:438.
Swarth, H. S. 1933. Off-shore migrants over the Pacific. Condor 35:40.
Thayer, J. E., and O. Bangs. 1908. The present state of the ornis of Guadaloupe (sic) Island. Condor 3:101–106.
Thoburn, W. W. 1899. The birds of Guadalupe Island. p. 278 *in* D. S. Jordan. The fur seals and fur-seal islands of the North Pacific Ocean. Pt. 3. United States Government Printing Office, Washington, D.C.
Todd, W. E. C. 1955. Taxonomic comment on races of Leach Petrel of the Pacific Coast. Condor 57:122.
Townsend, C. H. 1890. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross, No. XIV.—Birds from the coasts of western North America and adjacent islands, collected in 1888–89, with descriptions of new species. Proceedings United States National Museum 13:131–142.
———. 1911. (Account of expedition to lower California). Auk 28:390–391.
———. 1916. Voyage of the 'Albatross' to the Gulf of California in 1911. Bulletin American Museum Natural History 35:399–476.
———. 1923. Birds collected in Lower California. Bulletin America Museum Natural History 48: 1–26.
van Rossem, A. J. 1942. Preliminary comment on some Pacific Coast petrels. Proceedings Biological Society Washington 5:9–12.
von Berlepsch, H. G. 1906. On a new form of *Oceanodroma* inhabiting San Benito Island, off the coast of Lower California. Auk 13:185–186.

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